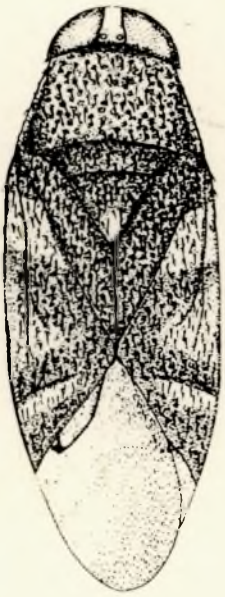
Aleksander Herczek

Systematic position of *Isometopinae* FIEB. *(Miridae, Heteroptera)* and their intrarelationships



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1.

Introduction

Isometopinae FIEB. constitute a small group of *Heteroptera* (family *Miridae*) with about 20 genera. With few exceptions, they live in tropical and subtropical regions. Hardly any information is available on their bionomy because they favour cryptic life habits. Their trophic preferences are not well explained either. Opinions range between the zoophagous and phyto-mecetophagous nature of *Isometopinae* FIEB. Some authors suggest that *Isometopinae* FIEB. are trophically associated with lichens and fungi whereas others that they are predators preying on minute insects. Trophic associations of *Isometopinae* FIEB. are extensively discussed by WHEELER and HENRY study (1977). Most of them are small insects not exceeding 4 mm. Modifications in head structure seem to be the most characteristic feature of their radiation processes.

The systematic position of *Isometopinae* FIEB. has been controversial ever since the taxon was created. Recently it has been proved beyond any doubts that they should be included into the family *Miridae*. However, their relations within this family have not been defined so far; neither have the intrarelations been studied in details. Within this taxon we lack morphological analyses of characters in terms of their plesio- or apomorphic nature. Accordingly, I have undertaken an attempt to analyse the characters in reference to the phylogeny of the group and to indicate the developmental lines within *Isometopinae* FIEB. General rules of the cladistic analysis were used. Some modifications were also introduced and discussed in the main part of the study.

I would like to express my gratitude to all my colleagues dealing with *Heteroptera* who encouraged me in carrying on the investigations. Special

thanks are directed to dr Bill R. Dolling, dr Thomas J. Henry, dr Izjaslav M. Kerzhner, dr Rauno Linnavuori, dr Syôiti Miyamoto, dr Carl W. Schaefer, dr Guy Smitz, dr Randall T. Schuh, dr James A. Slater, dr Gary M. Stonedahl and dr Mike Weeb for the loans of material. I am greatly indebted to dr Yuri A. Popov, whose remarks proved invaluable to my comprehension of the evolutionary processes in *Heteroptera*.

2.

Historical outline of faunistic and systematic studies on *Isometopinae* FIEB.

2.1. Systematic status

The family *Isometopidae* FIEB. was created by FIEBER in 1860 to comprise *Isometopus intrusus* (HERRICH—SCHAFER) and *I. alienus* FIEBER (FIEBER, 1860). Since then the rank and the systematic position of the group have remained controversial, FIEBER (1861) placed his family between *Coreidae* and *Phytocoridae* (the latter is one of the formerly used names of *Miridae* HAHN.). Several years later PUTON (1869) included the group into *Capsidae* (which also used to be a synonym of *Miridae*) in a rank of subfamily. In Puton's opinion *Isometopinae* FIEB. constituted a natural transition between *Capsidae* and *Pelogonidae (Ochteridea)*.

REUTER (1875) considered the group worth of a division rank (*Isometoparia*). However, the author himself withdrew from that opinion after a few years (REUTER, 1905). He decided to separate them from *Capsidae* at a family status. According to him *Isometopinae* FIEB. could not have been initial to *Capsidae* because some forms within the latter were older than those within the former. It was indicated, in Reuter's opinion, by a richer venation on forewing membrane and by the occurrence of the medial part of vein *M* (hamus) on hind wing in *Capsidae*.

REUTER's statements (1905) were supported by HANDLIRSCH (1906—1908), who, however, interpreted the relations between the two groups

differently. He assumed that *Isometopidae* FIEB. had been initial to *Capsidae* (Fig. 1). Reuter did not seem conviced and confirmed his former conclusions: he included the families *Isometopinae* FIEB. and *Miridae* HAHN. into the established series *Heteroptera* — *Anonychia* pointing to *Miridae* HAHN. as the more ancient group (REUTER, 1912). His definition was accepted by OSHANIN (1912), BERGROTH (1924), CHINA (1933), SPOONER (1938) and others. However, even at the time when Reuter's classification

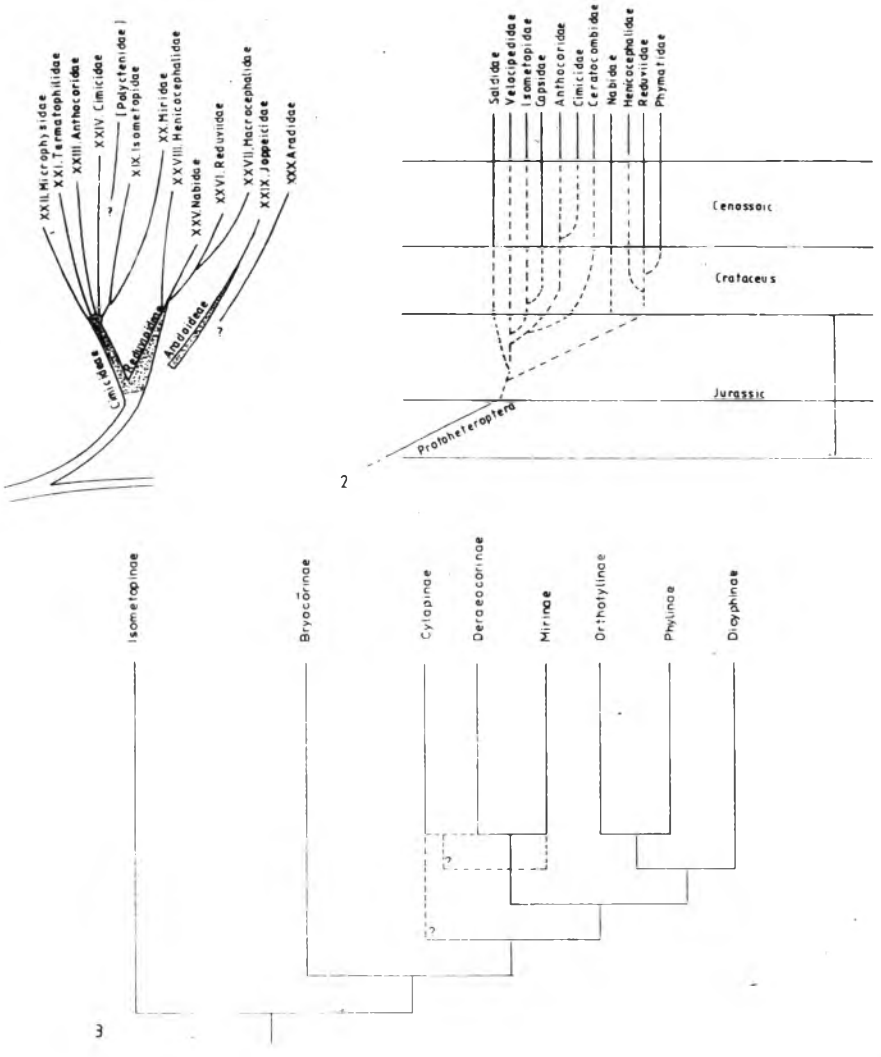


Fig. 1. A diagram of relationships of *Heteroptera* proposed by REUTER in 1910 (after KIRITSHENKO, 1951 — part)

Fig. 2. The relationships within *Heteroptera* according to HANDLIRSCH, 1908 (after KIRITSHENKO, 1951 — part)

Fig. 3. The relationships within *Miridae* as proposed by LESTON (1961)

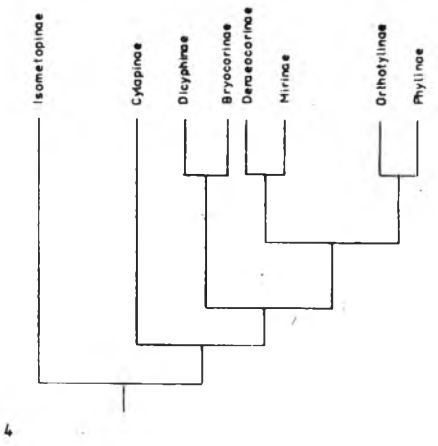


Fig. 4. A diagram of relationships of *Miridae* according to SCHUH (1974)

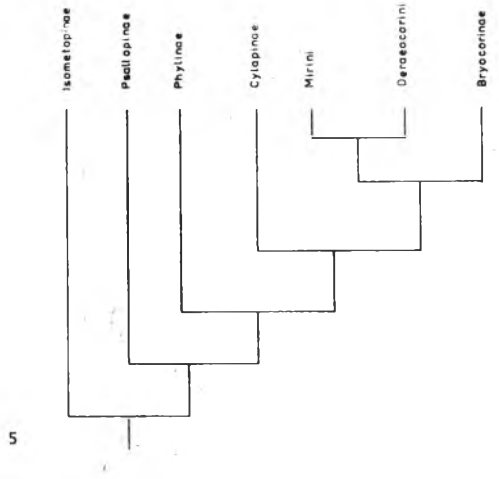


Fig. 5. The relations within *Miridae* according to SCHUH (1976)

prevailed, there were other suggestions regarding the position of the group. Some authors as, for instance, GIBSON (1917), McATEE and MALLOCH (1924), JORDAN (1941) recognized *Isometopinae* FIEB. as a subfamily within *Miridae*.

New morphological data, which were revealed in the following period, supported the idea of a close relation between *Isometopinae* FIEB. and *Miridae*. HESSE (1947) described the eggs of *Letaba bedfordi (Isometopinae)* and noted that they represented the same type as those of *Miridae*. SLATER (1950) found out that isometopinian sclerotic rings on dorsal walls of bursa

copulatrix and chitinous plates on posterior walls therein had structures similar to those in *Miridae*. On those grounds Slater concluded that *Isometopinae* and *Miridae* were related and the former were particularly close to *Phylinae* DOUG. and SCOTT.

CARAYON (1954, 1958) presented some strong arguments in favour of a close relation between *Isometopinae* FIEB. and *Miridae*. According to that author, both groups share the structure of rostrum and abdomen, wing venation, the structure of hemielytra and their membranes (with veins forming a single or two closed cells). In Carayon's opinion anatomical data proved quite informative: the relationship of the two groups seemed confirmed by a similar structure of female genitalia (copulatory organs), as had been previously noted by SCUDDER (1959). Moreover, Carayon argued that a two-segmented tarsus in *Isometopinae* FIEB. was not enough to grant them a separate status because the character was also encountered in other genera representing mirid subfamilies, for example in *Cylapinae* KIRK. and *Bryocorinae* BAEREN.; neither could the occurrence of ocelli be decisive for their independent position: Carayon stated that the reduction of ocelli was observed in different families. The latter argument was earlier put forward by CHINA and MEYERS (1929).

The recognition of *Isometopinae* FIEB. as a subfamily within *Miridae* was accepted by LESTON (1961), SLATER and SCHUH (1969), SCHUH (1974, 1976), ŠTYS and KERZHNER (1975), WHEELER and HENRY (1977), HENRY (1977), AKINGBOHUNGBE (1983) and others. All these authors pointed to some additional characters common to all *Miridae*.

Although the evidences seem quite convincing, some authors tend to interpret *Isometopinae* FIEB. as a separate family *Cimicomorpha* (KIRITSHENKO, 1951; CHINA and MILLER, 1959; SMITH, 1967; SMITZ, 1970; WAGNER, 1973; LINNAVUORI, 1975; GHAURI and GHAURI, 1983).

To the best of my understanding, the fact that *Isometopinae* FIEB. belong to *Miridae* is unquestionable. However, their position within *Miridae* is far from being precisely defined. LESTON (1961) made the first attempt to place *Isometopinae* FIEB. within the phylogenetic system of mirids. He assumed that the occurrence of ocelli testified an early separation from the ancestral group, which, in his opinion, contained nabidoidal forms. Leston did not interpret a single cell on membrane in numerous representatives of *Isometopinae* as indicating any relation to *Bryocorinae* (where a single cell is also retained). In his opinion, it was a case of analogy rather than homology. Leston presented his system in the form of a phylogenetic tree (Fig. 3).

SCHUH (1974) analysed intrarelationships of *Miridae* with the usage of HENNIG method (1966). He started with a statement that the evaluation of the characters used in the analysis, i.e. the decision whether they are apomorphic or plesiomorphic, was very difficult due to the relatively poor

understanding of mirid taxonomy. Schuh believed that among all *Cimicomorpha*, *Nabidae* COSTA retained most numerous plesiomorphic characters. Therefore, he analysed the structure of various elements in *Nabidae* and drew comparisons with *Miridae*. He assumed that if the character was expressed similarly in both groups, it should be interpreted as plesiomorphic. When, on the other hand, the character was differently expressed in *Miridae*, it must be treated as an apomorphy. Basing on such assumptions, Schuh was able to evaluate some characters in different mirid subfamilies (Tab. 1) and to construct the diagram of relationships within the *Miridae* family.

Table 1

Comparison of characters of subfamilies of *Miridae* according to SCHUH, 1974 (modified)

Condition \ Subfamilies	*Isometopinae*	*Cylapinae*	*Bryocorinae*	*Dicyphinae*	*Mirinae*	*Deraeocorinae*	*Orthotylinae*	*Phylinae*
Pronotal collar	*d*	*p—d*	*p*	*p*	*p*	*p*	*d*	*d*
Vesica	*p*	*p*	*p*	*p*	*p—d*	*p—d*	*p*	*d*
Posterior wall	*d*	*d*	*p?*	*d*	*d*	*d*	*d*	*d*
Sclerotized rings	*d*	*d*	*p?*	*d*	*d*	*d*	*d*	*d*
Number of tarsal segments	*d*	*p—d*	*p*	*p*	*p*	*p*	*p*	*p*
Feeding habits	*p*	*p*	*d*	*p—d*	*d*	*d*	*p—d*	*p—d*
Ocelli	*p*	*d*	*d*	*d*	*d*	*d*	*d*	*d*
Parempodia	*p*	*p*	*p*	*p*	*d*	*d*	*d*	*p—d*
Pulvilli (occurrence)	*p*	*p*	*d*	*d*	*d*	*p*	*d*	*d*
Pulvilli (position)	—	—	*i.s.*	*i.s.*	*v.s.*	—	*v.s.*	*v.s.*

Explanations: *p* — primitive; *d* — derived; *i.s.* — inner surface of claw; *v.s.* — ventral surface of claw

Also REUTER (1910; 1911—1912) distinguished between primitive and derived characters while discussing the relations amongst different groups of *Heteroptera* (Tab. 2). KERZHNER (1981) tried to list plesio- and apomorphic characters within *Cimicomorpha* (Tab. 3).

According to SCHUH (1974), *Isometopinae* constitute an isolated group within *Miridae*. As indicated by the presence of ocelli, it must have separated as the first one. Also *Cylapinae* branched off relatively early as testified by their predatory habits, relatively primitive structure of male and female genitalia, the lack of pulvilli and the occurrence of hair-like parempodia.

In 1976 SCHUH re-analysed the relationships within *Miridae*. Having evaluated many more characters (Tab. 4), he indicated synapomorphies in individual subfamilies and formed, on these grounds, particular groupings. His results were presented as a cladogram (Fig. 5). Schuh created the subfamily *Psallopinae* to contain the genus *Psallops* USING. Originally the latter

Table 2

Primitive and derived characters of *Heteroptera* according to REUTER, 1910 (after KIRITSHENKO, 1951)

Character	Primitive	Derived
Eyes	present	absent
Ocelli	present	absent
Antennae	4-segmented	5 or 3—1-segmented
Rostrum	4-segmented	3—1-segmented
Hemielytra	composed of 3 well-separated parts: cuticular clavus and corium membranous membrane (sometimes outer corium margin with embolium)	no separated parts of clavus, corium or membrane (homonomic)
Membrane	with numerous free veins or only partly formed closed cells	no venation
Meso- and metathorax	separate, metathorax with the openings of scent glands	not separate
Coxae III	articulated in one plane (pagiopodal)	articulated in several planes
Legs	of the same structure (homonomic)	of different structure (heteronomic)

Table 3

Some plesiomorphic and apomorphic conditions in *Cimicomorpha* (KERZHNER, 1981)

Condition	Plesiomorphic	Apomorphic
Microchaetae on head	present	absent
Antennal segments I and II	short	at most, segment II long
Posterior bridge of rostral plates	present	absent
Rostrum	of predatory type, penetrating	a) of predatory type for attack or blood sucking b) phytophagous
Sponge-like tibial sole	absent	present or reduced
Tarsus	3-segmented	2-segmented
Hemielytral hypocostal plate	shifted from the margin	margin
Costal fracture	present	absent
"Alive" membrane venation	4 closed cells	a) 3 cells not in contact with cuneus b) 2 cells touching cuneus c) 1 cell not in contact with cuneus d) longitudinal vein at base e) absent

Table 3 cont.

Condition	Plesiomorphic	Apomorphic
Abdominal segment VIII in male	normally developed	more or less reduced
Parameres	symmetrical	asymmetrical or missing
Ovipositor	lanceolate	different
Genital apophysis	absent	a) present b) reduced
Spermatheca	normally developed	a) reduced, non-functional b) modified into a larval gland c) absent
Parastigmal foveae	absent	a) present b) reduced
Trophacytes maturation	late	early
Feeding	predatory	a) phytophagous b) blood sucking on warm-blooded forms

belonged to the subfamily *Phylinae* but was excluded from it by CARVALHO (1956), who suggested that the genus was related to *Isometopinae*. However, in *Psallops* USING. there are no ocelli, which made the union with *Isometopinae* impossible. Its position was not decided until Schuh's diagnosis. According to Schuh, *Isometopinae* are a sister group in relation to all other *Miridae*. The synapomorphic character shared by all the remaining *Miridae* was represented by the reduction of ocelli. For Schuh, the monophyletic character of *Isometopinae* was indicated by the following apomorphies: reduced number of femoral trichobotria, modified head and strongly enlarged eyes (especially in males). A successive developmental line of *Miridae* was constituted by *Psallopinae*. However, Schuh did not mention any apomorphies of that group.

Different opinion on phylogenetic relations of mirid subfamilies was presented by SCHUH and SCHWARTZ in 1984. They commented critically on earlier systems and suggested that *Isometopinae*, *Psallopinae* and *Cylapinae* should constitute a single clad with the occurrence of the subapical tooth on claws as a plesiomorphic character shared by the three groups.

The first subdivision of *Isometopinae* (then in the rank of a separate family) was presented by BERGROTH in 1924. The author distinguished two subfamilies: *Diphlebinae* and *Isometopinae*. Diagnostic characters of *Diphlebinae* included: a very short but broad pronotum (more than four times as broad as long), scutellum with a distinct medial ridge, and cuneus which almost reaches the apex of forewing membrane; cuneus is markedly longer than broad, and has its inner margin sickle-like incised. Also two veins on forewing

Characters used in construction of interrelationships of *Miridae* (according to SCHUH, 1976)

Plesiomorphic state	Apomorphic state
1. Head usually not strongly flattened or elongated; eyes usually not greatly enlarged, although often slightly larger in males than females	Head modified, often flattened or elongated dorso-ventrally; eyes, especially in males, often greatly enlarged and touching or nearly so on vertex
2. Generally six mesofemoral, seven or eight metafemoral trichobotria	Trichobotrial numbers greatly reduced, two mesofemoral, three metafemoral trichobotria
3. Ocelli present	Ocelli absent
4. Parempodia setiform	Parempodia often lamellate and convergent apically
5. Vesica of males membranous, inflatable to at least a limited extent; phallotheca attached to phallobase	Vesica of males straplike, rigid, not inflatable except for partially membranous areas; phallotheca not attached to phallobase
6. Eight metafemoral trichobotria	Seven metafemoral trichobotria, "1a" absent
7. Subapical claw tooth present	Subapical claw tooth absent
8. Claw hairs usually present	Claw hairs absent
9. Pulvilli absent	Pulvilli usually present and attached to ventral surface of claw
10. Anterior margin of pronotum finely upturned	Anterior margin of pronotum in form of rounded collar
11. Subapical claw tooth present	Subapical claw tooth absent
12. Dorsum usually impunctate	Dorsum often heavily punctate
13. Vesica of male inflatable often without spiculi; secondary gonopore poorly developed	Vesica of male inflatable, with many spiculi, and well-developed secondary gonopore
14. Posterior wall of female simple (but see Othotylini)	Posterior wall of female variously modified
15. Parempodia setiform	Parempodia lamelliform, apically divergent
16. Generally six mesofemoral, eight metafemoral trichobotria	Trichobotrial numbers often greater than six on mesofemur and eight on metafemur
17. Claws not strongly toothed basally	Claws strongly toothed basally
18. Tarsi not dilated distally	Tarsi generally dilated distally
19. Tarsal guard setae short	Tarsal guard setae usually very long
20. Membrane usually with two cells	Membrane usually with one cell

membrane, which occupy almost entire space and do not form closed cells, were treated as typical of *Diphlebinae*. *Isometopinae*, on the other hand, were defined by pronotum, which is three times as broad as long, and cuneus, which is as broad as or slightly broader than its length, rarely reaching beyond half forewing length and has a straight inner margin.

Bergroth partitioned *Isometopinae* into two divisions: *Isometoparia* and *Myiommaria*. *Isometoparia* were distinguished on scutellum much longer than broad (as in many *Pentatomidae*) and reaching the inner basal corner of membrane, and the occurrence of clavus which tapers toward its apex and does not form the claval commissure (*commissura clavale*) along the line where the right and left wings meet. The second division, *Myiommaria*, is typically provided with scutellum broader than its length or almost equilateral, or with clavus of parallel or divergent sides which form distinct claval commissure along the line of the wing contact.

McATEE and MALLOCH (1932) adopted the division presented by Bergroth, but they changed the ranks: *Isometopinae* became a subfamily, in which the *Diphlebini* and *Isometopini* tribes were distinguished. The latter tribe was further subdivided into *Myiommaria* and *Isometoparia*. A slightly modified version was presented by AKINGBOHUNGBE and HENRY (1984), suggesting that *Myiommaria* should be raised to the tribal rank. They, however, did not present any evidences which would justify such a decision. Presently, McAtee and Malloch's division has remained the only one that illustrates the relationships within *Isometopinae*.

2.2. History of faunistic studies

Apart from *Isometopus*, Fieber's family *Isometopidae* included the genus *Myiomma* PUT., which was described by PUTON (1872). Till the end of XIXth century the family *Isometopidae* FIEBER received some new species of *Isometopus* FIEBER (*I. mirificus* MULSANT and REY, 1887; *I. heterocephalus* PUTON, 1898; *I. teaniaticeps* PUTON, 1898). UHLER (1891) included the description of *Heidemania cixiiformis* into his work, but he overlooked that the form possessed ocelli and did not place the species within the family.

At the beginning of the XXth century DISTANT (1904) described the fauna of India, Burma and Ceylon and created the genera *Sophianus* and *Turnebus* with the type species *S. alces* and *T. cuneatus* respectively. KIRKALDY (1908) introduced the Australian genera *Eurycrypha* and *Nesocrypha (E. thanatochlamys, N. corticola)*. In the same year HEIDEMANN (1908) described three new American species of *Isometopus* (FIEB.): *I pulchellus, I. signatus* and *I. unicolor*.

Thanks to the works of DISTANT (1910a, b), POPPIUS (1913, 1915) and GIBSON (1917) the number of known genera and species of *Isometopinae* FIEB. has been significantly enlarged. Distant described the genera *Jehania*

and *Scapana*. Poppius created the genera *Isometopidea*, *Turnabiella* and *Lidopus*. Gibson, in turn, described new species in the genera *Myiomma* PUT. and *Isometopus* FIEB. (*M. media* GIB. and *I. liberatus* GIB.).

In 1922 McATEE and MALLOCH created a new genus, *Corticoris*, to contain the American species of *Isometopus* described by Heidemann. Two years later they described further genera (*Wetmora* and *Alcecoris*) and a new species (*Lidopus schwartzi*) (McATEE and MALLOCH, 1924). The same authors presented data on further representatives of *Isometopinae:* the new genus *Ptisca* and the new species *Isometopus bicolor* and *I. peltatus*. Also BERGROTH (1924) described the genera *Diphleps* and *Teratodia*.

The genus *Isometopus* FIEB. was then extended to receive the new species *I. canariensis* LIND., *I. kaznakowi* KIR., *I. japonicus* HASEG. and *I. hananoi* HASEG., described by LINDBERG (1936), KIRITSHENKO (1939) and HASEGAWA (1946) respectively.

In late forties HESSE (1947) erected a new genus *Letaba* and presented extensive information on the bionomy of *L. bedfordi* HESSE. CARVALHO (1947) described the genera *Aristotelesia* and *Plaumanocoris*. A few years later he established the genera *Paramyiomma* (with the species *P. lansburyi* and *P. hemialba*), *Lindbergiolla*, *Biliola* and *Bilionella* and a new species *Alcecoris globulosus* (1951). HOBERLANDT (1952, 1959) added *Paramyiomma duodenensis*, *P. affinis*, *P. milleri* and *Linbergiolla jarmilae* to the list and CARVALHO and SAILER (1954) described a new genus *Isometocoris*. The new genus was distinguished on the occurrence of two pairs of ocelli. Successive studies (HENRY and MALDONADO CAPRILES, 1982), however, indicated that those structures were in fact the remnants of hair on head and did not correspond to the typical isometopinal ocelli. Accordingly, *Isometocoris* CARV. and SAIL. was placed in another subfamily (*Psallopinae* SCHUH) (HENRY and MALDONADO CAPRILES, 1982).

The list of *Isometopinae* FIEB. was considerably extended by LINNAVUORI (1962), CARVALHO and ROSAS (1962), HSIAO (1964) and MIYAMOTO (1965), who described the following new forms: *Isometopus diversiceps* LIN., *I. tijaninus* HSIAO, *I. fasciatus* HSIAO, *I. hainantus* HSIAO, *I. hasegavai* MIYAM., *Paramyiomma surinamensis* CARV. and ROS., *Myiomma samuelsoni* MIYAM., *M. minutum* MIYAM. SMITH (1967) erected a new genus *Magnocellus* to contain two species: *M. wacriensis* and *M. ghanaiensis*, which were later recognized as the representatives of the two generic groups of *Magnocellus* (AKINGBOHUNGBE, 1983). Moreover, Smith reported eight new species of the genus *Myiomma* PUT. (*M. rubra*, *M. impunctata*, *M. fulva*, *M. verticata*, *M. rubroventata*, *M. albiscutellata*. *M. nigra* and *M. fasciata*) and described *Letaba nitida*.

At the turn of the sixties and seventies SLATER and SCHUH (1969) described further species within the genera *Magnocellus* SMITH, *Letaba*

HESSE, *Myiomma* PUT. and *Isometopidea* POPP., WAGNER (1973) within the genus *Isometopus* FIEB., LINNAVUORI (1975) within *Magnocellus* SMITH, *Isometopus* FIEB. and *Myiomma* PUT., and SLATER (1976) within *Myiomma schmitzi*. Also in 1976 BRAILOVSKY described a new species of the genus *Wetmora*. HENRY (1977) presented some new species of *Diphleps* BERGH. and, together with HERRING (1977), described new species of *Corticoris* McATEE and MALLOCH. Somewhat later, he added new species to the genus *Myiomma* PUT. and created new genera *Lidopiella* and *Myiopus* (HENRY, 1979; 1980).

To boot, the genus *Totta* (GHAURI and GHAURI, 1983) was added to *Isometopinae* FIEB. A further significant contribution to the knowledge of *Isometopinae* was provided by AKINGBOHUNGBE (1983), who presented new representatives of *Magnocellus* SMITH.

Also American representatives of *Corticoris* McATEE and MALLOCH proved to be more numerous: HENRY (1984) described *C. pallidus, C. pintoi* and *C. pubescens*. He also presented some data on a new species of *Myiomma* PUT.: *M. keltoni* HENRY. In 1984 CARVALHO reported on the genus *Joceliana* in Brazil.

KERZHNER (1987) described two new species of *Isometopus* FIEB. from the far east of Russia, *I. amurensis* and *I. rugiceps*. REN SHUZI and YANG CHI-KUN (1988) presented two Chinese species of the same genus *(I. marginatus* and *I. beijingensis)*, and also *Sophianus lamellatus* and the genus *Paraletaba*. POLHEMUS (1988) reported on the first representative of *Isometopinae* from Madagascar, i.e. *Magnocellus madagaskariensis*. In 1990 SCHWARTZ and SCHUH presented *Gigantometopus rossi*, which is the largest species known so far, and exhibits some strange morphological attributes. Two years later *Isometopus ovatus* was described (HERCZEK, 1992).

With the increasing number of known genera and species, the understanding of their relationships and their systematic positions began to change. For instance, HEIDEMANN (1908) included the species *Heidemania cixiiformis* UHLER into *Isometopinae* FIEB. and stated that the form was closely related to the genus *Myiomma* PUT. The information was confirmed by REUTER (1912), who recognized the genus *Heidemmania* UHLER as a junior synonym of *Myiomma* PUT. Also McATEE and MALLOCH created a new genus, *Corticoris*, which contained all the precisely examined American species of *Isometopus*. Later they (McATEE, MALLOCH, 1924) included *Myiomma media* GIBSON into this group and suggested that *Corticorus liberatus* (GIBS.) might represent a colour variation of *C. unicolor* (HEID.). They also assumed that *Teratodia emoritura* BERG. was a synonym of *Diphleps unica* BERG. and that the differences described by BERGROTH (1924) resulted from sexual dimorphism and the bad condition of the examined specimens. McATEE

and MALLOCH (1932) recognized the genera *Turnebus* DIST., *Skapana* DIST. and *Palonella* POPP. as synonyms of *Isometopus* FIEB. and the genus *Turnabiella* POPP. as synonymous with the genus *Bilia* DIST. They also suggested a close relation between *Eurycrypha* KIRK. and *Isometopus* FIEB.

CARVALHO (1925) treated the genera *Jehania* DIST. and *Letaba* HESSE as synonymous with *Isometopus* FIEB. The synonymy of *Letaba* was further confirmed by LINNAVUORI (1975), who declared that the location of ocelli cannot be the only distinguishing character on the generic level and pointed to the genus *Isometopus*, within which different locations can be found. His opinion, however, was not commonly accepted. For instance, SMITH (1967) regarded the differences between *Letaba bedfordi* HESSE and *L. nitida* SMITH on one hand, and *Isometopus* FIEB. on the other, valid and important enough to justify the placement of the species in different genera. He also synonymized the genus *Paramyiomma* CARV. with the genus *Myiomma* PUT (SMITH, 1967).

CARAYON's paper (1985) provided new data about some species of *Isometopinae* FIEB. and included *Bilia* DIST., *Biliolla* CARV. and *Bilionella* CARV. into *Anthocoridae* FIEB.

In 1977 HENRY confirmed McAtee and Malloch's opinion about the synonymy of *Teratodia* BERG. and *Diphleps* BERG. The author commented also that the report on *Diphleps unica* BERG., which appeared in MALDONADO CAPRILES's paper (1969), referred in fact to a new species *D. maldonadoi* HENRY. Moreover, he created in 1980 a new genus *Brailovskicoris*, to contain the species *Wetmora nocturna*, which was described by BRAILOVSKY (1978). HENRY and CAPRILES (1982) suggested that *Isometocoris blantoni* CARV. and SAIL. should be placed in the subfamily *Psallopinae* SCHUH because it did not have ocelli.

AKINGBOHUNGBE (1988) suggested further modifications of the classification of *Isometopinae* FIEB. In his opinion *Letaba* HESSE is a synonym of *Paloniella* POPP. and some species of the genus *Magnocellus* should be actually placed in the genus *Isometopus* FIEB. The remaining species were included into a new genus *Smithopus* AKING. Additionally, Akingbohungbe created a new genus *Slateropus* AKING. for the species *Isometopidea miriformis* SLATER and SCHUH. Unfortunately, those statements were not supported by any precise data.

The genus *Paraletaba*, described by REN and YANG (1988), was included at a subgeneric rank into *Isometopus* FIEB. (HERCZEK, 1991). Besides *I. (P) montana* REN and YANG, the subgenus contained *I. (P) ovatus* HERCZEK. However, further examination indicated that the latter was different enough to be granted a generic status as *Paratopus* gen. nov., which is described in the present study.

3.

Distribution of recent *Isometopinae* FIEB.

The zoogeographical information on *Isometopinae* has not been analysed so far. Their recent distribution or the history of their radiation have not been examined at length either. The former question has been roughly dealt with by EYLES (1971), who discussed the distribution of recent genera in relation to geographical regions in a short chapter of his study. Further studies will surely add new genera and species to the present list of subfamily representatives, and the pattern of their distribution might be slightly modified. However, major characteristics of their distribution do not seem liable to any major changes, regardless of the number of the newly described forms.

Within the tropical belt, from which most *Isometopinae* have been reported (Fig. 6), two centres of the genus abundance can be delineated (the division of the tropical regions into provinces follows ŠTYS's system, 1981). The first centre is located in the Ceylon province of the Oriental region (with the southern part of Indian Peninsula included). The representatives of 6 genera have been reported from this centre (out of the total 8 genera known so far from the Oriental region). The second centre is situated in the W. African province and 5 genera have been described from there. The abundance of genera is unquestionable if we realize that in other provinces of the Ethiopian region only 1 to 3 genera are represented, each of which is also known from the W. African province. The W. African centre is also exceptionally rich in species: 23 species are reported from the area, which is more than from any other zoogeographical unit of the same rank in the world. Other areas of a relatively numerous species representation include a part of the Oriental

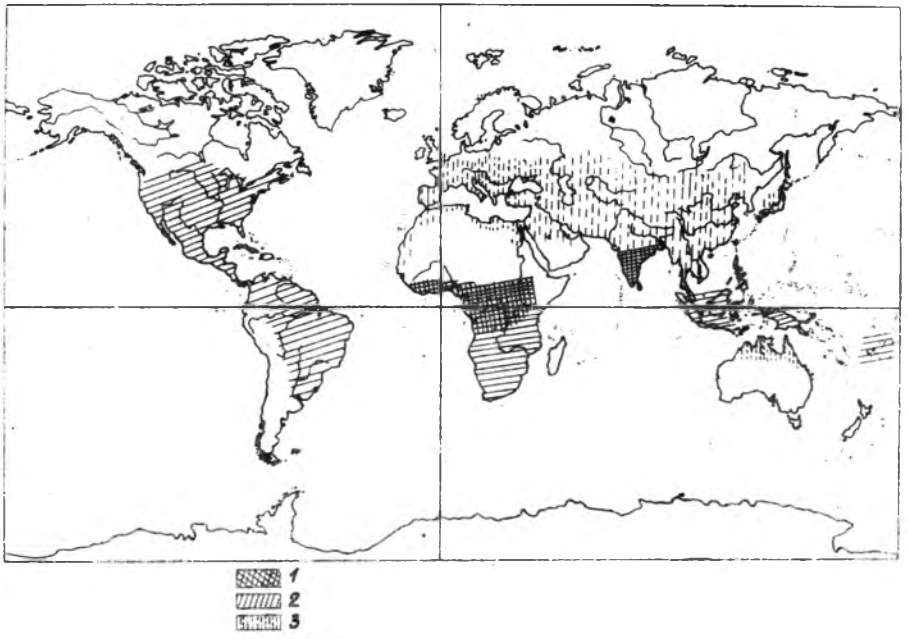


Fig. 6. Distribution and the abundance centres of *Isometopinae*
1 — 5—6 genera, 2 — 4—3 genera, 3 — 2—1 genera

region (the Ceylon and Indochinese provinces) and the Brazilian province of the Neotropical region. In the Oriental centre it seems noteworthy that in the Ceylon province the number of species is only slightly higher than that of genera whereas in the Indochinese province nine out of ten species belong to a single genus (*Isometopus* FIEB. — constituting its centre of radiation). In the Ceylon province the genus is represented by only one species and in the provinces of other regions at most three representative species of *Isometopus* have been reported.

Distributional patterns of various genera of *Isometopinae* indicate that the centres of radiation coincide with the ones of differentiation. It is manifested by the fact that a large proportion of the genera known from the radiation centres represents endemic groups. Accordingly, in the Ceylon province four out of six known genera are endemic, in the W. African two out of five, in the Brazilian province three out of four and in the Polinesian province of the Australian region all three known genera are endemic.

In recent fauna two most numerous tribes *Isometopini* and *Myiommini* are different in their distributional characteristics. Most genera of *Isometopini* are reported from the W. African province (i.e. four out of five, with the only genus outside this province being the Australian province endemite). One of them, *Isometopus*, enters the Oriental region (where in the Indochinese

province it has a substantial species representation). *Myiommini*, on the other hand, have several centres of abundance. The Ceylon province is one of them (with four genera, three of which are endemic) and the Mexican-Central American province (with six and four genera respectively). Only the genus *Myiomma* seems to be widely distributed among *Myiommini* and it is reported from the most warm and temperate warm provinces in all regions except for the Australian one.

The question about the original distribution of *Isometopinae* remains open. It seems that the answer has become possible thanks to description of the Eocene representatives of this subfamily. The Eocene (except its final spans) enjoyed warm (tropical or subtropical) climate, which did not differ significantly from the one of the Cretaceous period. Climatic differences were at that time less dramatic than later and therefore distributional ranges of groups were much wider (ESKOV, 1987). Accordingly, it can be suspected that *Electromyiommini* were very widely distributed. The same holds true for *Myiommini*, which are also known from the Baltic amber. It is further confirmed by the recent polycontinental distribution of that tribe. The climatic changes which took place at the turn of the Eocene and Oligocene reduced the ranges and limited their world distribution to the equatorial zone, where *Isometopinae* underwent further differentiation in each geographical region separately (because of the isolation). Thus endemic genera and species were developed, such as *Totta* (reported only from the Oriental region) or *Plaumancoris* and *Joceliona* (restricted in their distribution only to the Brazilian region). In turn, a limited range of the genus *Gigantometopus*, which is reported only from the Malaysian province of the Oriental region, represents probably its relict range because the tribe *Gigantometopini* represents a sister group in relation to all other tribes — so it must have existed in the Eocene and, alike other groups, it must have had a relatively wide range, although it need not have been either quite diverse or numerous.

In the southern provinces of the Palaearctic region (division after KOSTROWICKI, 1965) there are only few species of the genera *Myiomma* PUT. and *Isometopus* FIEB. They seem to be relatively young species, which proved so invasive as to acquire secondarily the areas of the subtropical and temperate warm zones.

4.

Fossil *Isometopinae* FIEB.

Fossil materials are quite important in phylogenetic considerations. They also help determine when particular taxa originated. First fossil *Miridae* were described from the Upper Jurassic: *Miridoides mezozoicuss* B-M and POP. (BECKER-MIGDISOVA and POPOV, 1963) and *Scutellifer karatavicus* POP. (POPOV, 1968). In the studies by Scudder, Heer, Cockerell, Shatz and others, mirid representatives of the Cenozoic fauna are described from different areas of North America, Western Europe and Asia. A substantial amount of forms has been found in the Baltic amber dating back to the Eocene (GERMAR and BERENDT, 1856; CARVALHO, 1954, 1966; CARVALHO and POPOV, 1984; JORDAN, 1944; HERCZEK, 1991a, b; HERCZEK and GORCZYCA, 1991). Fossil *Isometopinae* are first reported from the amber inclusions from Mexico (HURD, SMITH and DURHAM, 1962). Other descriptions of the subfamily and the closest related *Psallopinae* refer to the Eocene. In the Eocene Baltic amber, the representatives of both subfamilies were found and identified (POPOV and HERCZEK, 1993a, b; HERCZEK and POPOV, 1993). Also the new representative of the subfamily *Isometopinae*, which is described in this paper, has been found in the Baltic amber.

All known Eocene genera and species of *Isometopinae* were characteristically provided with a two-segmented tarsus and a reduced anal vein within the inclusion part of the hemielytra: these are apomorphies peculiar to the developmental line of *Isometopini* and *Myiommini*. The retention of clypeus cutting into the frons and the occurrence of the vein $R+M$ running parallelly to the anterior wing margin in the hind wings allow to recognise those genera as representing the older developmental line, which is in a sister relation to both tribes *(Isometopini* and *Myiommini)*, and to create a new tribe

Electromyiommini trib. nov. to comprise them. The new tribe includes the following genera: *Electromyiomma* POP. et HERCZ., *Metoisops* POP. et HERCZ., *Clavimyiomma* POP. et HERCZ., and the genus *Archemyiomma* sp. n. described in this paper.

Although no representatives of *Isometopinae* have been reported so far from the Upper Jurassic period, we have to assume that they existed at that time as a sister line in relation to all other taxa of *Miridae* (some of which were described from the Upper Jurassic materials). It should be noted that in sedimentary rocks only the imprints of hemielytra are well-preserved and, because they lack apomorphies on the subfamily level, it is often difficult to identify the subfamily. Furthermore, it cannot be excluded that some imprints may have been erroneously classified. Accordingly, only the finding of the imprint from the Upper Jurassic, in which the characters of the head capsule would have been preserved, would constitute the direct evidence that *Isometopinae* had existed at that time.

The new tribe *Electromyiommini*, the representatives of which were found in the Baltic amber, represents a sister group in relation to the *Isometopini* — *Myiommini* clad (Fig. 100), and therefore must have existed in the same period. The same holds true for the members of the tribe *Gigantometopini*. Moreover, in the Baltic amber the representative of *Isometopinae* was found which undoubtedly belongs to the genus *Myiomma* (POPOV and HERCZEK, 1993). This indicates that by that period all the distinguished subtribes had already developed (I assume that the tribe *Gigantometopini*, which retains most plesiomorphies and constitutes a sister line in relation to *Electromyiommini*, had its representatives in the fauna). Nevertheless, it must be emphasized here that no fossil representatives of the tribe *Isometopini* have been described so far. It might be less surprising if we realize that even in the recent fauna they do not constitute the most numerous representation either.

5.

New taxa of *Isometopinae* FIEB.

Totally, 22 genera (including the genus *Diphleps*) are included into the subfamily *Isometopinae*. The genera form two tribes: *Diphlebini* and *Isometopini* (McATEE and MALLOCH, 1932). The latter tribe was subdivided into *Myiommaria* and *Isometoparia*. The examination of some recent and fossil materials yielded the identification and descriptions of several new genera and species belonging to the subfamily *Isometopinae*. Thanks to these new data and the detailed morphological analysis, it was possible to arrive at the modified division of *Isometopinae*.

5.1. New genera and species

Archemyiomma gen. nov.

Diagnosis: Body elongated. Head orthognathic, almost as broad as high and twice as broad as long. Anterior part of pronotum somewhat convex, calli not defined.

Legs slender, only femora III slightly thickened but not so stout as in recent species of *Isometopinae*.

Type species: *Archemyiomma carvalhoi* sp. n.

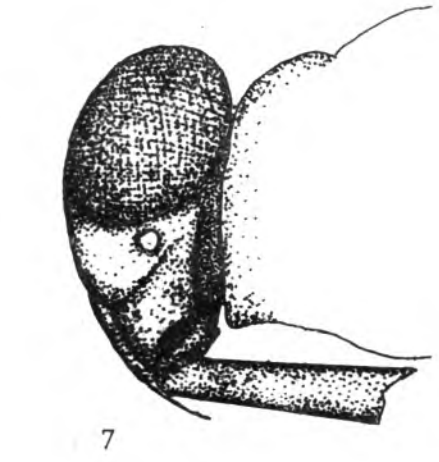
Derivatio nominis: the generic name combines the Greek "Arche", which means "old", with the recent name of the genus *Myiomma*.

Comparative notes: The new genus is similar to the genus *Metoisops* POP. and HERCZ., from which it differs in the shape of bigger eyes, much longer

first segment of rostrum, longer and narrower pronotum and in deeper and denser microstructure of pronotum and hemielytra. Moreover, in the new genus there are no calli, whereas they are present in *Metoisops*.

***Archemyiomma carvalhoi* sp. nov.**

Diagnosis: Body 3 mm in length, brown, slightly shining, with head, pronotum, mesoscutum and scutellum slightly darker. Forewing membranes dark. The underside of the body dark brown in colour. Dorsal surface covered with long, bright hairs, which become denser on pronotum.



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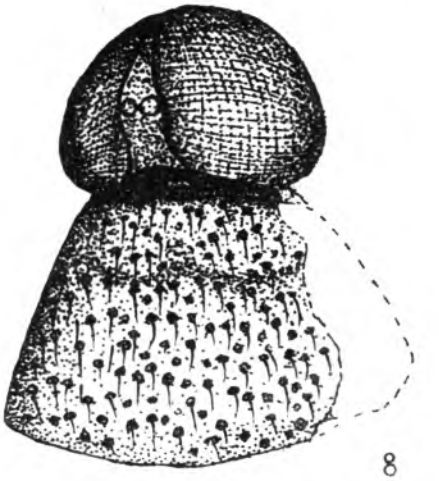

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Figs. 7–8. *Archemyiomma carvalhoi* sp. n.
7— head in lateral view, 8 — head and pronotum in dorsal aspect (somewhat laterally)

Eyes convex, slightly raised above the vertex, in the frontal part separated by the distance somewhat longer than the ocellus diameter. Ocelli proportionally large, strongly protuberant, occupying the central part of vertex and lying in contact with the inner margins of eyes. Frons moderately convex, clypeus slightly bent backwards. Rostral segment I reaching half length of the coxae I. Antennae cylindrical with the first segment as thick as the second. Antennal segments III and IV somewhat thinner than segments I and II. Antennal segment III almost twice as short as VI.

Pronotum without the apical collar, deeply punctate, with the straight anterior margin and the posterior one slightly convex. Mesoscutum partly open, scutellum shorter than its width at base. Hemielytra somewhat brightened, covered with grooves which are shallower and sparser than those on pronotum. Claval commissure 1.5 times as long as

the scutellum length. Subcostal field (embolium?) relatively narrow but well-marked; cuneus distinctly defined, almost as long as broad. In hind wings vein R+M parallel to the anterior wing margin (Figs. 7, 8).

Metric data (in mm): Body: length — 2.70, width — 1.14; head: width — 0.6, length — 0.28, height — 0.57; eye: width — 0.20, height — 0.28; vertex width — 0.10; ocellus diameter — 0.04; antennal segment lengths: I — 0.21, II — 0.83, III — 0.26, IV — 0.41; rostral segment lengths: I — 0.31, II — 0.37, III — 0.31, IV — 0.32; pronotum: width — 0.77, length — 0.57; scutellum: width at base — 0.50, length — 0.39; claval commissure length — 0.65; leg III: femur: length — 0.98, width — 0.23; tibia: length — 1.17, width — 0.05; tarsus segment lengths: I — 0.12, II — 0.31.

Holotype: ♂, Amber Inclusia, Hemiptera. In. 181000, Samland No. 478. Brit. Mus. Nat. Hist., London.

Derivatio nominis: The species name has been chosen as a tribute to J. C. M. Carvalho, who is an outstanding specialist in *Miridae*.

Paratotta gen nov.

Diagnosis: body elongated, almost three times as long as its width. Head somewhat raised above pronotum, orthognathic, slightly broader than the anterior margin of pronotum and nearly three times as short as its height. Frons strongly elongated dorso-ventrally, bent backwards. Genae narrow, shifted backwards in relation to the frons. Antennal segment II spindle-shaped, slightly arcuate. Pronotum almost twice as broad as long, laterally flattened narrowly in a carinate manner, with the arcuate incised posterior margin. Scutellum small, slightly broader than long.

Type species: *Paratotta orientalis* sp. n.

Derivatio nominis: The generic name was coined by "para", which means "closely", and the name of the recent genus *Totta* GH. and GH., to which the described genus is morphologically similar.

Comparative notes: the new genus resembles the genus *Totta* GH. and GH. in the structure of frons, location of antennae and the incision of the inner eye margin. It differs from the latter in the head raised above the pronotum level, narrower genae, arcuate incision of the posterior pronotum margin, somewhat larger eyes and in the structure of the antennal segment II, and the general colouration of the body. Modifications in the head capsule structure attribute this genus to the generic group *Totta* of the subtribe *Tottina* subtrib. nov.

Paratotta orientalis sp. nov.

Diagnosis: Ground colour fuscous. Head, eyes, the first, the second and two thirds of the third segment of labium and most underside of the body

rusty-brown. Antennal segment I, terminations of rostral segments III and IV and scutellum termination yellow. Antennal segment II slightly brightened at both ends. Hemielytra with pale yellow stripes below the basal part and at the base of cuneus and slightly brightened within the medial part of exocorium. Legs pale yellow except femora and tibiae III, which are fuscous with only apices yellow. Body mat (except slightly shining and punctate pronotum), covered with decumbent, brown hair, some of which (over the bright parts of hemielytra) is yellowish. Membrane finely rugose longitudinally, smoked. The smaller cell on the membrane is well-defined.

Body elongated, oval, 2.4 mm in length. Head about 2.8 times as broad as its length. Interocullar distance somewhat larger than the ocellus diameter. Antennae set concentrically above the lower eye margins, with segment I slightly longer than its width. Pronotum relatively narrow, with the length to width at base ratio 0.55, slightly raised in the middle part. Anterior margin of pronotum slightly convex, posterior one broadly concave. Lateroposterior parts of pronotum truncate and slightly flattened.

Hemielytra with a well-defined subcostal field and membrane covered with very short hairs and provided with two closed cells (Figs. 9—13).

Metric data (in mm): Body: length — 2.4, width — 0.84; head: width — 0.51, length — 0.19, height — 0.64; eye width (on the line with ocelli) — 0.19; vertex width — 0.13; ocellus diameter — 0.04; pronotum: width at base — 0.78, length — 0.44; scutellum: length — 0.25, width — 0.32; antennal segment lengths: I — 0.06, II — 0.78, III and IV missing; rostral segment lengths: I — 0.21, II — 0.23, III — 0.23, IV — 0.22; leg III: femur: length — 0.78, width — 0.21; tibia: length — 1.24; first tarsal segment length — 0.07; II — 0.19; claval commissure length — 0.33; cuneus length — 0.28.

Holotype: ♂, Laos, Vientiane Prov., Ban Van Eue, 30 September 1967. Native Collector Bishop. Bishop Museum, Honolulu.

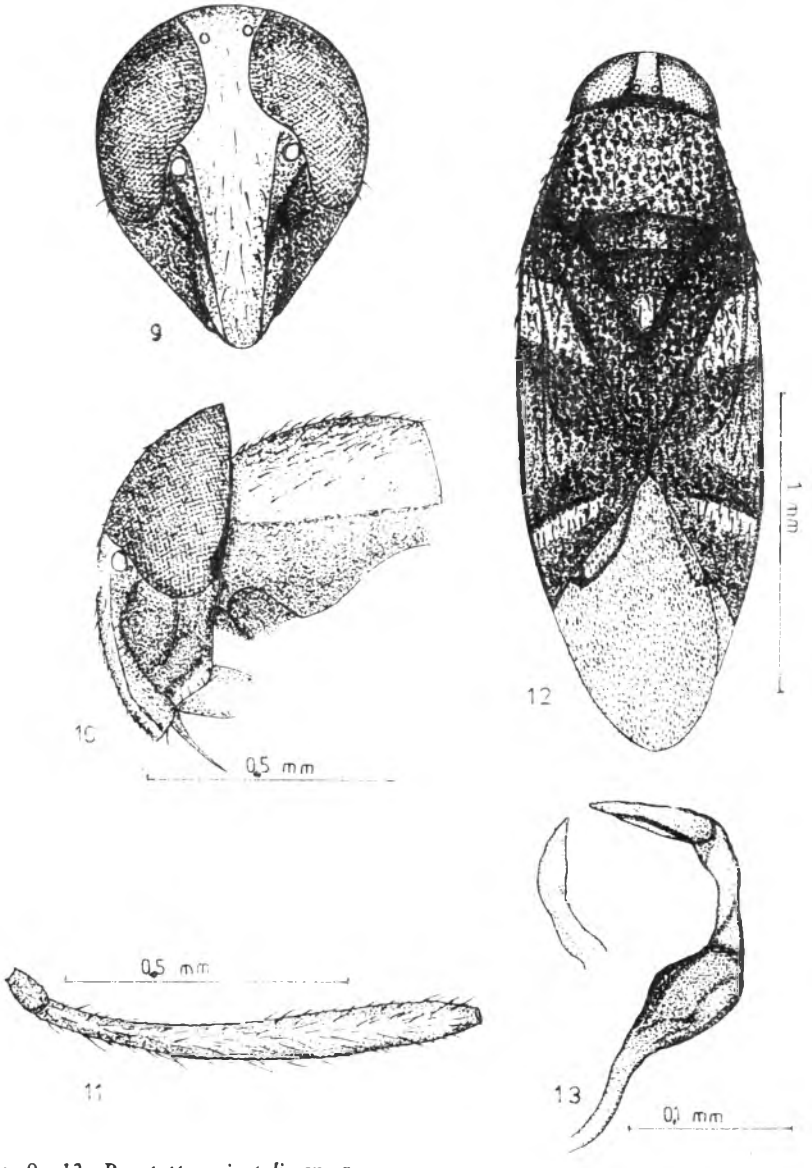
Paratype: 1 ♂, Borneo (Brit. N.), Sandakan Bay (SW), Sapagaya Lumber Camp 2—20 m, 1 January 1957, Alpina, leg J. L. Gressitt. Bishop Museum, Honolulu.

The paratype is somewhat brighter than the holotype with red-brownish tinge dominating. In the paratype vertex is slightly narrower (0.11 mm) and pronotum is both shorter and narrower (0.36 mm and 0.69 mm respectively). Antennal segment II and rostral segment II are also somewhat longer (0.82 mm and 0.27 mm respectively.).

Derivatio nominis: the species name is derived from the late Latin word "orientalis", which means "eastern".

Popovia gen nov.

Diagnosis: body elongated, oval. Head strongly flattened frontally. Frons broad, strongly expanded to sides, enclosing the eyes, bent backwards with



Figs. 9—13. *Paratotta orientalis* sp. n.

9 — head in frontal view, 10 — head and pronotum in lateral view, 11 — antennal segments I and II, 12 — general appearance, 13 — parameres

a markedly reduced, flat clypeus located on the underside. Genae strongly depressed, shifted under the frons surface to a considerable extent.

Half way on cuneus a distinct transverse bulge (in form of a convex roller).

Forewing membrane with two celli; the smaller one strongly reduced and opened to the cuneus apex.

Type species: *Popovia fijiensis* sp. n.

Derivatio nominis: The generic name was coined in honour of Y. A. Popov, who is an eminent heteropterist.

Comparative notes: The new genus resembles the genus *Magnocellus* SMITH, from which it differs in almost entirely flat fronto-clypeal part of the head, retention of the shortened claval commissure, the occurrence of the distinct transverse bulge on cuneus and in a strongly reduced smaller cellus, which opens to cuneus on wing membrane.

Popovia fijiensis sp. n.

Diagnosis: ground colour yellowish brown, head dirty yellow, eyes and ocelli reddish-brown. Antennae yellow, pronotum yellowish, somewhat darker anteriorly and densely covered with brown spots. Mesonotum brown, darker in the middle part, punctate. Scutellum yellowish, in its subapical part brown and, alike pronotum, covered with brown spots. Hemielytra with a pale yellow stripe along the radial vein. Clavus much darker than scutellum, densely punctate. Cuneus mostly pale yellow. Above the cuneal fracture, in humeral corners and at the apex of cuneus brown patches are distributed. Forewing membranes mat, smoked, with brighter veins and covered in dense, very fine hairs, which are visible under the microscope. Body covered with bright brown, decumbent pubescence except antennal segments III and IV, which are clothed with brighter and slightly erect hairs.

Body ellipsoidally elongated, flattened dorso-ventrally. Head twice as wide as its length and about 1.3 times as wide as high. Lateral eyes separated from the head margin. Interocullar distance slightly larger than half the diameter of the ocellus. Clypeus small, retained in the lower part of frons, not extending beyond the frons surface. Antennae set well beyond the lower eye margins. Antennal segment I three times as long as its diameter and slightly arcuate. Antennal segment II basally thinner than the first one and apically thickened. Antennal segment III slightly longer than the half length of antennal segment II, without any thickened area; segment IV spindle-like, twice as short as antennal segment III.

Rostrum reaching the apex of ovipositor.

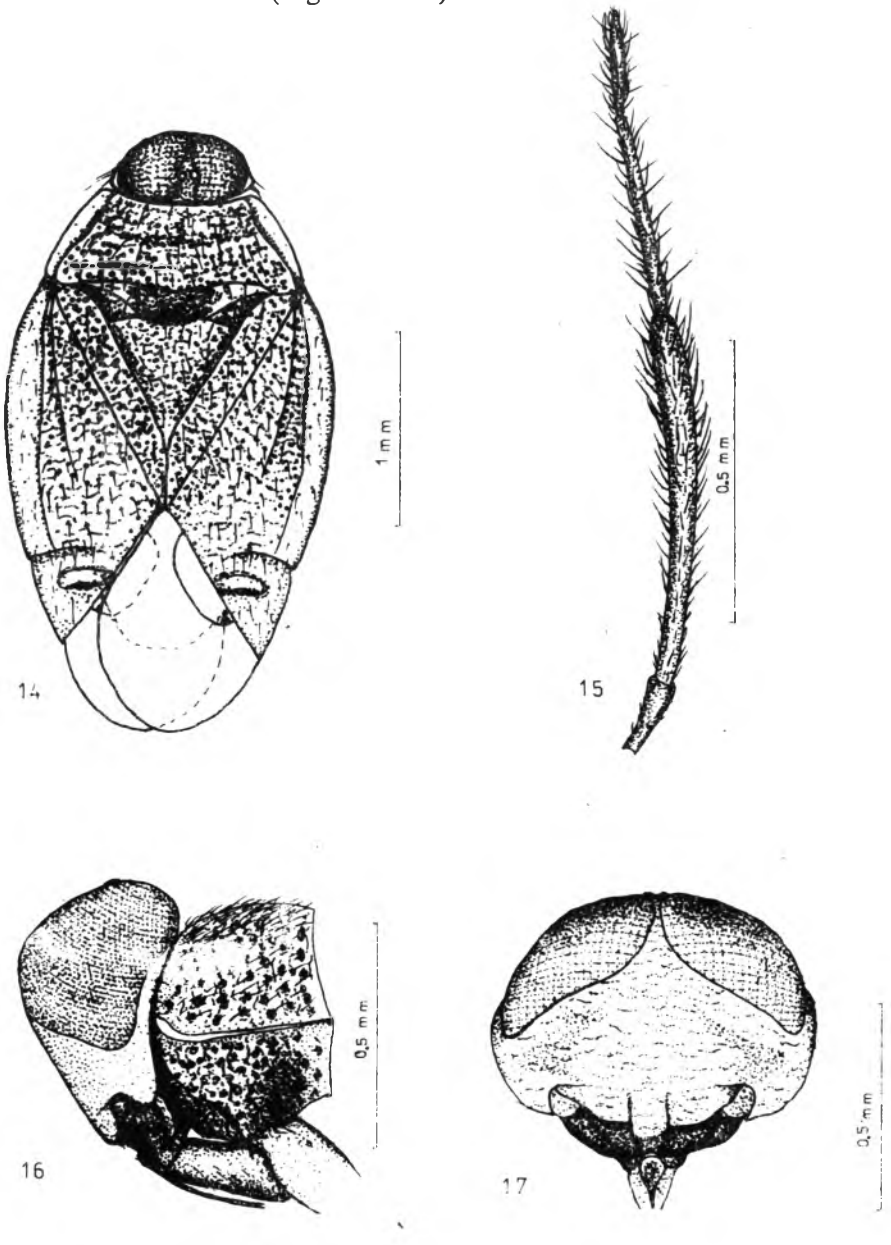
Pronotum 2.8 times as wide as long, with the anterior margin slightly concave and the posterior one bisinuate incised. Lateral fragments carinate flattened, straight.

Mesonotum exposed, slightly raised above the enlarged scutellum.

Hemielytra with a wide subcostal field (embolium?) reaching half cuneal fracture length. Cuneus with a very distinct, transverse, roller-shaped bulge in the middle part.

Vein $R+M$ on hind wings reduced, taking form of a short, stump-like process.

Femora III strongly thickened, only 2.8 times as long as wide, provided with three trichobotria (Figs. 14—17).



Figs. 14—17. *Popovia fijiensis* sp. n.

14 — general appearance, 15 — antenna, 16 — head and pronotum in lateral view, 17 — head in frontal view

Metric data (in mm): Body: length — 3.25, width — 1.6; head: width — 0.73, length — 0.36, height — 0.58; eye width and height (in line with ocelli) — 0.35; vertex width (in line with ocelli) — 0.10; ocellus diameter — 0.04; pronotum: width at base — 1.25, length — 0.45; scutellum length and width — 0.68; antennal segment lengths: I — 0.13, II — 0.68, III — 0.38, IV — 0.43; leg III: femur: length — 0.93, width — 0.33; tibia length — 1.25; tarsal segment lengths: I — 0.12, II — 0.24; ovipositor length — 0.75.

Holotype: ♀ Belt Road, 20 mi W. of Suva, Viti Levu, Fiji, Beating shrubs, 23 July 1938, EC Zimmerman Collector, Bishop Museum, Honolulu.

Derivatio nominis: the species name was based on the place of collection, i.e. Fiji Islands.

Fronsonia gen. nov.

Diagnosis: Body broadly oval. Frons slightly convex. Clypeus totally relegated from frons, shifted to the underside of the head, where it takes an almost horizontal position. Genae small, strongly shifted backward behind the frons. Eyes occupy almost entire head surface, laterally reaching upon proepipleurum.

Pronotum with a straight anterior margin. Cuneus with the inner margin covered with long, stout hairs.

Type species: *Fronsonia ochracea* sp. n.

Derivatio nominis: The name draws attention to the species habitus — "frons".

Comparative notes: the new genus is similar to the genus *Nesocryha* KIRK. especially in the morphology of the frontal head part and also in the reduction of vein $R+M$ on hind wings and the retention of a shortened claval commissure. It differs from the latter in the straight anterior margin of pronotum, the fact that cuneus is not enlarged, the occurrence of long and stout hairs on the inner margin of cuneus and in larger eyes, which reach upon proepipleurites.

Fronsonia ochracea sp. n.

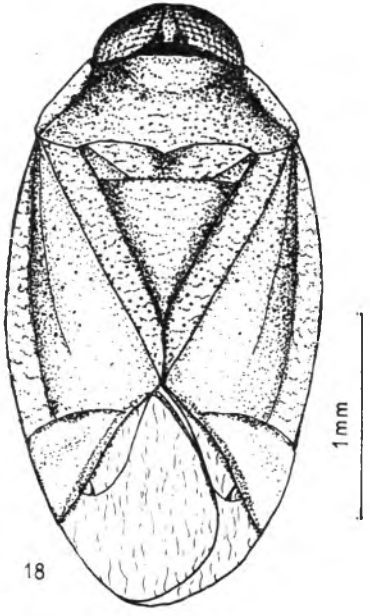
Diagnosis: ground colour pale tawny. Head and eyes fuscous with a red tinge. Antennae fuscous, antennal segment I termination, antennal segments III and IV slightly brightened. Pronotum mat, with eight brown spots in the anterior part and fine brown punctae all over its surface. Mesoscutum darker in the middle. Scutellum concolourous with pronotum, with a small brown patch in the apical part and brown spots all over its surface. Hemielytra punctate, clavus bright brown, the rest of hemielytra somewhat brighter, whitish at places. The basal part of hemielytra along the cuneus and apical fragments of cuneus fuscous. Membrane mat, slightly smoked. Coxae yellowish. Femora

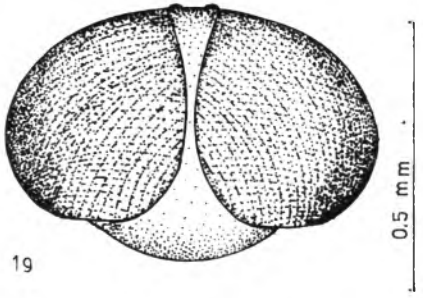
I and II alike. Femora III yellowish at bases, subapically brown and apically yellow with a red band. Tibiae and tarsi brown. Body pubescence tawny, on antennal segments III and IV brighter.

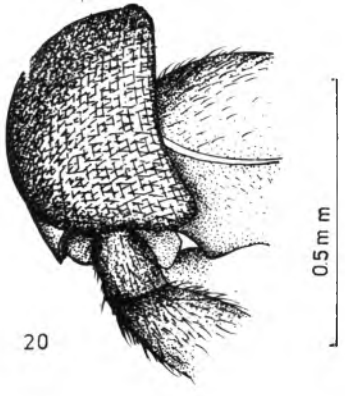
Head with the frons poorly protruding, about 2.8 times as wide as long and 1.6 times as wide as its height. Eyes extremely large, frontally in contact with one another. Ocelli located near the posterior margin of vertex, in contact with the eyes. Frons strongly bent backwards with the lower margin broadly arcuate. Antennae set well below the lower, inner corners of eyes, with segment I short (only slightly longer than its diameter). Antennal segment II thicker than I, densely covered with semi-erect hairs, which are shorter than the segment diameter; antennal segments III and IV very short, thin, subequal in length, covered with semi-erect hairs.

Pronotum 2.6 times as wide as long, with the anterior margin straight and the posterior margin bisinuate incised. Lateral pronotal parts carinate flattened, lateroposterior corners truncate.

Scutellum enlarged, slightly convex anteriorly.







Figs. 18—20. *Fronsonia ochracea* sp. n.

18 — general appearance from above, 19 — head in frontal view, 20 — head and a fragment of pronotum in lateral view

Hemielytra with a broad, flattened subcostal field (embolium?).

Femora III strongly thickened, with the length to width ratio 3:1. Tibiae slender, tarsus 2-segmented, segment I as long as segment II. Claws slightly bent with a subapical tooth (Figs. 18—20).

Metric data (in mm): Body: length — 2.8, width — 1.5; head: width — 0.70, length — 0.25, height — 0.43; eye width (on line with ocelli) — 0.38; vertex width (on line with ocelli) — 0.15; ocellus diameter — 0.05; pronotum: width at base — 1.25, length — 0.48; scutellum: length — 0.65, width at base — 0.62; antennal segment lengths: I — 0.10, II — 1.03 (0.09 in diameter), III — 0.13, IV — 0.1; femur III: length — 0.90, width — 0.30; tibia III length — 1.05; tarsal segment III length — 0.20.

Holotype: ♂, Nandiravatu, Viti Levu, Fiji, 15 September 1938, 2700", at light, EC Zimmerman Collector, Bishop Museum, Honolulu.

Paratype: 1 ♂, Fiji Islands, Suva, 1.4.1940, R.A. Lewer, British Museum; 1 ♂., Fiji Islands, Suva, 10.9.1938, R 323, R.A. Lewer, British Museum, London.

Derivatio nominis: the species name draws attention to the body colouration which is typical of the species.

Jozefus gen. nov.

Diagnosis: body oval. Head flattened frontally, as wide as high. Frons slightly bent backwards, from the line of lower eye margins showing stronger tendency to incline backwards. Clypeus strongly shortened, restricted to the frons underside but not raised above the frons plane. The apical segment of rostrum longer than the remaining ones (the longest).

Type species: *Jozefus guineiensis* sp. n.

Derivatio nominis: The generic name was based on the Polish first name "Jozef", in honour of the author's father.

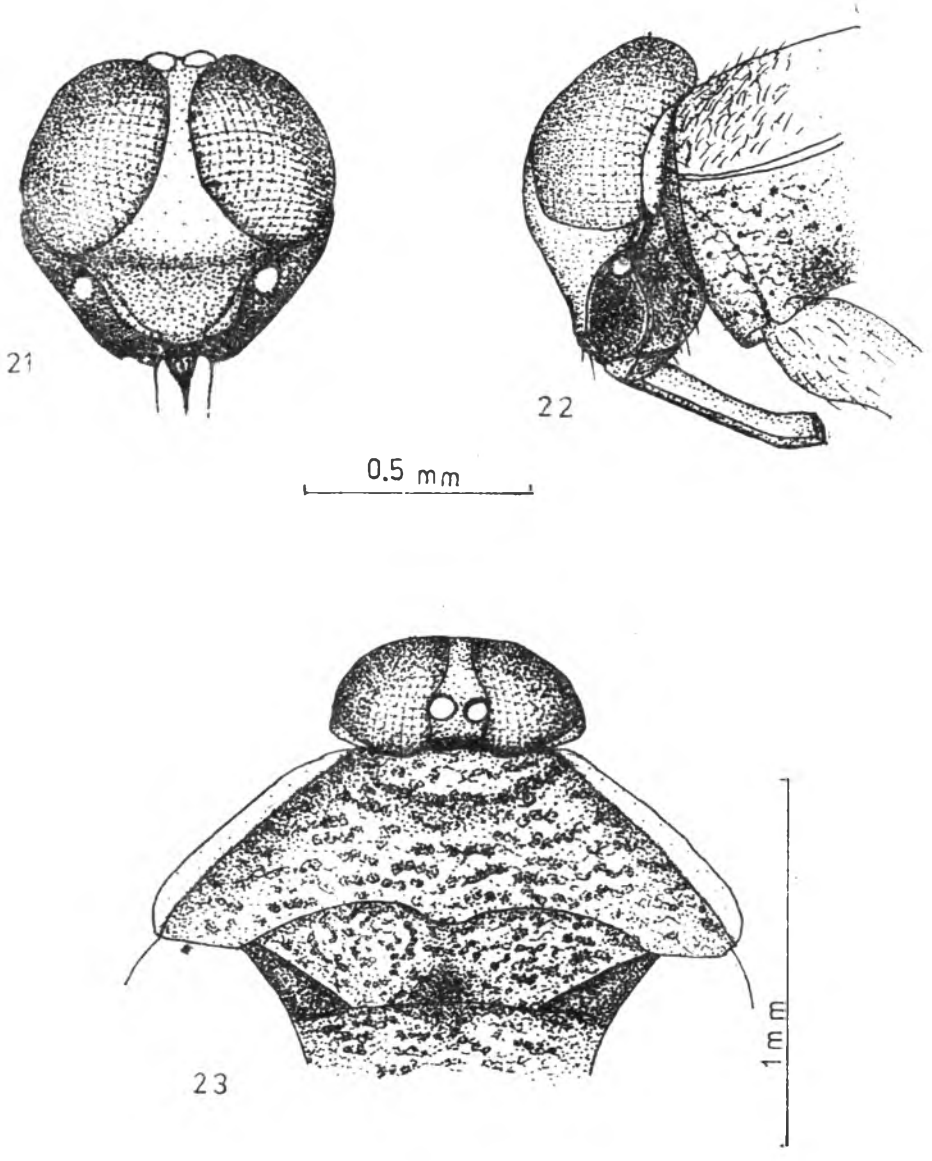
Comparative notes: The new genus resembles the genus *Popovia* gen. nov., but differs from the latter in the structure of frons, the shape of eyes, the antennal pubescence and morphology, the shape of pronotum, much longer apical rostral segment and in the colouration.

Morphological characters of the new genus suggest that it should be included into the subtribe *Nesocryphina* subtrib. nov. within the tribe *Isometopini*.

Jozefus guineiensis sp. n.

Diagnosis: ground colour of the body brown. Eyes reddish brown with two black bands in the anterior inner part. Ocelli fuscous. Vertex and frons tawny, genae fuscous. Antennal segment I and the basal part of the second tawny, the remaining part and segments II and IV brown. Pronotum mat, with a brighter

medial field and four darker patches at base; two patches are located centrally and two laterally. Sides of pronotum carinate, flattened, bright, semi-transparent and shining. Mesonotum and scutellum fuscous, the latter adorned with a longitudinal brighter band running from the base to the apex and with fuscous patches in the medial part laterally. Scutellum apex brown. Hemielytra brighter in the middle and fuscous at the area bordering on the cuneal fracture



Figs. 21—23. *Jozefus quineiensis* sp. n.

21 — head in frontal view, 22 — head and a fragment of pronotum in lateral view, 23 — head and pronotum from above

(cuneus termination also fuscous in colour). Forewing membrane grey, mat, covered by delicate pubescence and fuscous veins. The whole body punctate (deeper punctae located on mesoscutum, scutellum and clavus), covered with brown hair, which is very short on the frons.

Body broadly oval and twice as broad as its length. Among the facettes fine, short hairs are detectable under the microscope. Ocelli large, lie in contact with the inner eye margins. Frons with a marked short clypeus in the lower part. Antennae set below the lower eye margins, with a small, thickened segment I. Antennal segment II cylindrical, bearing two types of hair: semi--decumbent, shorter than the segment diameter and strongly erect, almost twice as long as its diameter. Antennal segment III 3.6 times as short as II; segment IV slightly spindle-shaped, twice as short as III. The last two segments clothed with hairs resembling those on a segment II. Rostrum reaching half abdomen length.

Pronotum 3.5 times as wide as long. Its sides convex, carinate, flattened, moderately truncate towards the middle in posterior part. Scutellum 1.2 times as long as its width, slightly convex. Hemielytra with a broad subcostal field reaching half length of the cuneal fracture (Figs. 21—23).

Metric data (in mm): Body: length — 3.88, width — 2.0; head: width — 0.71, length — 0.35, height — 0.70; eye width and height (in line with ocelli) — 0.26 and 0.45 respectively; vertex width (in line with ocelli) — 0.19; ocellus diameter — 0.09; pronotum: width at base — 1.73, length — 0.50; scutellum: width — 0.80, length — 0.91; antennal segments lengths: I — 0.15, II — 1.08, III — 0.30, IV — 0.15; rostral segments lengths: I — 0.38, II — 0.50, III — 0.45, IV — 0.58.

Holotype: ♂, New Guinea: NE Mt. Kaindi, 2350 m, 8 January 1973, J. L. Gressitt Collector. Bishop Museum, Honolulu.

Derivatio nominis: the species name indicates the place of collection of the type species.

Paratopus gen. nov.

Diagnosis: Body broadly oval, convex, especially so in front of the declivous membrane. Pronotum hidden almost to its half length under the obliquely overlying head. Clypeus strongly reduced, persisting only on the underside of the frontal plate. Hemielytra with a broad subcostal field reaching two thirds of their length, distinctly shining. The line of wing contact short but well-defined.

Type species: *Paratopus ovatus* (HERCZ.).

Derivatio nominis: The generic name was coined by joining word "para", with means "close", and the last syllables of the generic name, *Isometopus*.

Comparative notes: The type species description and comparative remarks can be found in the study on the synonymized species — *Isometopus ovatus* (HERCZ.) (HERCZEK, 1991).

Magnocellus SMITH, 1967

Diagnosis: The generic description was presented in Smith's study (1967).
Type species: *Magnocellus wacriensis* SMITH.

Magnocellus longisetosus sp. n.

Ground colour pale tawny. Posterior head margin and frons pale yellow. Eyes, ocelli with adjacent fragments of vertex, latero-posterior part of the head from the line of the lower part of eyes brightly red. Antennal segment I pale yellow, II somewhat darker. Pronotum with anterior and posterior parts darker. Mesonotum orange yellow in colour; scutellum alike with the sides at mid point and the apex white and with the subapical part darkened. Hemielytra with a brightened basal part and a brown posterior part (as well as the base of cuneus). Forewing membrane grey, slightly smoked. Legs yellow, with darker tibiae (especially in legs III). Femora I bear a brown patch in the subapical portion dorsally. A much larger patch of the same tinge located on the outer side of the subapical part of femora III.

Body covered in decumbent, long, yellow pubescence, which is especially dense on clavus and hemielytra. Mesonotum and scutellum covered by semi-decumbent, tawny hair. Short and sparse blackish brown hair scattered on the frons. Membrane with fine, dense and pale yellow pubescence visible under the microscope.

Dorsum of the body punctate: deeper spots on clavus, shallower on mesoscutum and scutellum. Punctation on pronotum rather shallow, bright brown, denser posteriorly. Frons bright brown spotted; the pattern rather weak.

Body oval, flattened. Head frontally flat, 2.5 times as wide as its length and 1.3 times as wide as its height. Eyes enlarged, not in contact with posterio-lateral head margins, frontally almost touching one another and occupying more than half head height. Ocelli large, in contact with eyes, interocellar distance half their diameter.

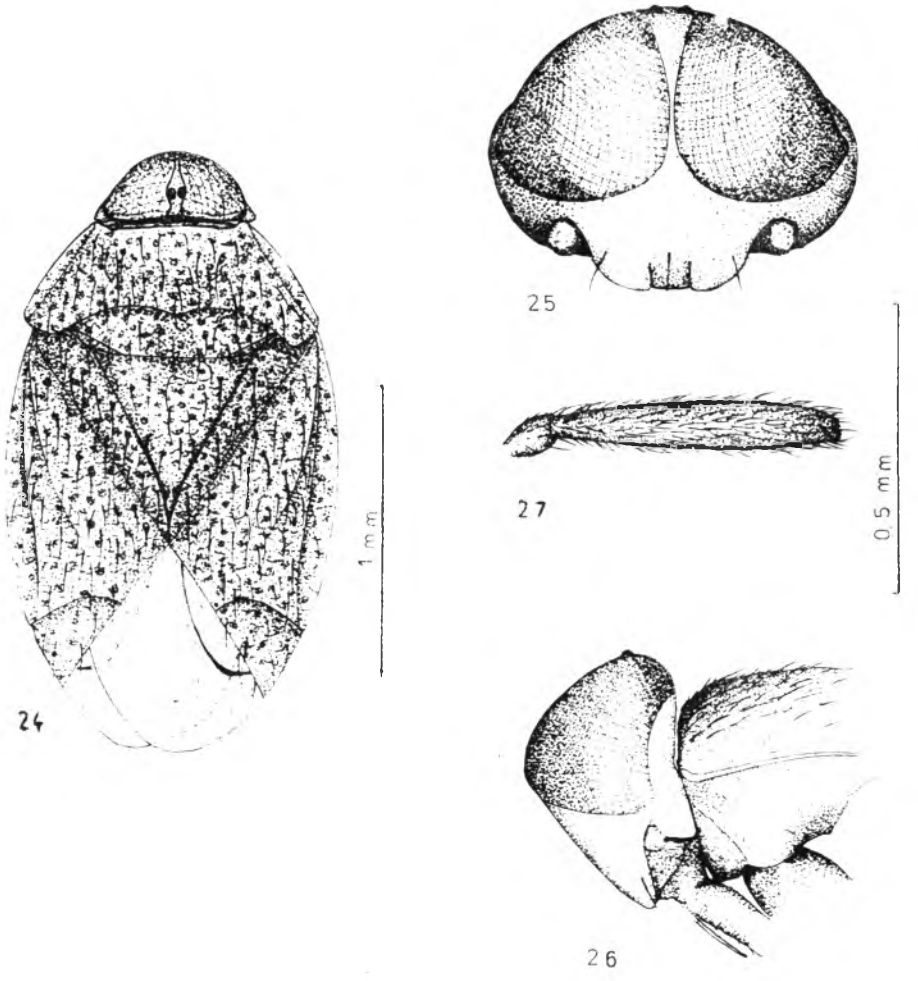
Frons strongly bent backwards with a very short clypeus delineated on the underside. Genae developed under the frons surface, broad. Antennae set below lower eye margins. Antennal segment I short, thickened; II — as thick as I; segments III and IV — missing in the described specimen. Rostrum reaching beyond coxae III.

Pronotum without the apical ring, 3.1 times as wide as its length, with an extremely narrow, flat collar and the posterior margin bisinuate. Its sides

convex, narrowly flattened. Latero-posterior sides broadly truncate. Mesoscutum open, depressed in medial part, obviously separate from scutellum. Scutellum slightly protuberant, as long as wide, enlarged and elongated with a sharp apex.

Hemielytra with a subcostal field (embolium?) flattened, somewhat broader in medial part. Forewing membrane bears a single closed cell.

Femora III thickened, with the length to width ratio 2.5. Tibiae slender, tarsi 2-segmented, with the first segment twice as short as the second. Claws slightly bent, with a well-marked subapical tooth (Figs. 24—27).



Figs. 24—27. *Magnocellus longisetosus* sp. n.

24 — general appearance; 25 — head in frontal view; 26 — head and a fragment of pronotum in lateral view; 27 — antennal segments I and II

Metric data (in mm): Body: length — 2.15, width — 1.23; head: width — 0.58, length — 0.23, height — 0.45; eye width and height (in line with ocelli) — 0.11; ocellus diameter — 0.04; pronotum: width — 1.8, length — 0.35; scutellum length and width — 0.60; antennal segment lengths: I — 0.10, II — 0.50, III and IV — missing; rostral segments lengths: I — 0.23, II — 0.20, III — 0.33, IV — 0.23; leg III: femur: length — 0.75, width — 0.30; tibia length — 0.95; tarsal segment lengths: I — 0.10, II — 0.18.

Holotype: ♂, Salomon Is. Florida Is., Nddela I. Haleta 0—100 m., 6 October 1964, R. Strattman, Malaise Trap, Bishop Museum, Honolulu.

Derivatio nominis: The generic name was coined with Latin words "longus" (long) and "setae" (bristles) and draws attention to the pubescence type on hemielytra.

Comparative notes: the described species was included into the group "*ghanaiensis*" SMITH. It is close to *Magnocellus ghanaiensis* SMITH, 1967, but differs from it on the pronotum, mesoscutum and scutellum colouration, the structure of frons and eyes, and the head width to length ratio. In the new species the anterior part of the body is not brown or white, whereas in *M. ghanaiensis* one third of mesonotum and the distal part of scutellum are chocolate brown and the basal half of pronotum is white. Pronotum width to length ratio in *M. ghanaiensis* SMITH is 3.3:1, whereas in the new species it is expressed by 2.5:1 value. Also the antennae are differently set in either species: in *M. longisetosus* sp. n. the bases of antennae are located just below the lower eye margin, whereas in *M. ghanaiensis* SMITH they lie at a reasonable distance from it. Moreover, hairs covering each form is of different length.

5.2. A survey of the tribes and subtribes within *Isometopinae* FIEB.

Gigantometopini trib. nov.

Diagnosis: Body elongated, about 7 mm in length. Calli distinct, separated by a deep incision. Scutellum strongly swollen, heart-like in shape. On clavus a vestigal vein 1A. On femora II and III 5 and 6 trichobotria in succession. Tarsi 3-segmented; claws without a subapical tooth.

Electromyiommini trib. nov.

Diagnosis: Body elongated, 2—4 mm in length. Fronto-clypeal part of head not expanded dorso-ventrally or laterally. Clypeus well-marked, not shifted

from the frons. Eyes enlarged, separated from anterio-lateral margins of pronotum. Ocelli in a distance from the posterior head margin. Pronotum with a marked, narrow and flattened collar (the collar differs morphologically from that in *Deraeocorinae* and *Mirinae*). Calli usually distinct, divided by a median groove.

Vein $R+M$ in hind wings not shortened, running parallelly to the anterior wing margin.

The tribe houses most fossil genera described so far: *Electromyiomma* POP. et HERCZ. (type genus), *Clavimyiomma* POP. et HERCZ., *Metoisops* POP. et HERCZ. and *Archemyiomma* gen. nov.

Isometopini FIEBER, 1860

Diagnosis: Body broadly oval, flattened dorso-ventrally. Frons expanded laterally, frontally flattened. Genae and clypeus pushed to the underside of the head capsule. Scutellum strongly enlarged, claval commissure strongly shortened or absent. Vein R in hind wings straight and relatively long.

Type genus: *Isometopus* FIEBER.

Isometopina FIEBER, 1860

Diagnosis: clavus with convergent sides, the line of wing contact absent, scutellum reaching the inner corner of membrane base. Vein $R+M$ on hind wings not reduced, directed towards the wing margin.

Nesocryphina subtrib. nov.

Diagnosis: clavus with sides parallel or slightly convergent, the line of wing contact distinct although considerably shortened. Vein $R+M$ on hind wing reduced to a stump-like process.

Type genus: *Nesocrypha* KIRK.

Myiommini BERGROTH, 1924

Diagnosis: body elongated, not flattened dorso-ventrally. Head with frons not expanded laterally. Genae and clypeus frontally visible, at least in part. Scutellum not enlarged, clavus of parallel or divergent sides. Vein R in hind wings shortened and arcuate.

Type genus: *Myiomma* PUTON.

Plaumanocorina subtrib. nov.

Diagnosis: Mesoscutum completely or partly hidden. Cuneus strongly reduced.

Type genus: *Plaumanocoris* CARV.

Tottina subtrib. nov.

Diagnosis: Frons narrowly flattened dorso-ventrally. Clypeus fused with frons. The inner eye margin with a reniform incision. Antennae set centrally, above the lower eye margins.

Type genus: *Totta* GH. and GH.

Myiommina BERGROTH, 1924

Diagnosis: Frons not narrowed. Clypeus not fused with frons, eyes with a straight inner margin.

Type genus: *Myiomma* PUT.

6.

Characteristics and evaluation of morphological characters

In order to determine phylogenetic relations among taxonomic units it is necessary to define which attributes are apomorphic and which plesiomorphic in nature. Accordingly, morphological analysis of *Isometopinae* seemed inevitable.

Apomorphies of *Miridae* were searched for by comparing the structure of individual elements in various groups of *Cimicomorpha*. The scheme of relations presented by SCHUH and ŠTYS (1991) was incorporated as the basis for further considerations. According to these authors, *Microphysidae* DOHRN are a sister group in relation to all other *Miriformes*. *Thaumastocoridae* KIRK., in turn, constitute a sister line in relation to the clad of *Miridae* and *Tingidae* LAPORTE *sensu lato* (Fig. 28). Additionally, the structure of the analysed elements was compared with that in the representatives of *Nabidae*; it is an old group, which, according to many authors, retained most numerous plesiomorphies within *Cimicomorpha*. When a similar type of structure was found in all those groups but in *Miridae*, the variant unique to *Miridae* was regarded as apomorphic in the latter. Alike, if the same type of structure in sister lines was typical of some *Miridae*, it was regarded as plesiomorphic while the other variant (peculiar to the remaining *Miridae*) was considered as apomorphic in the groups endowed with it. It must have always been proved that the changes did not take place parallelly even in closely related groups. However, it seemed reasonable to introduce the notion of a secondary apomorphic character when similar structural changes occurred parallelly in different developmental lines. The notion was already used by

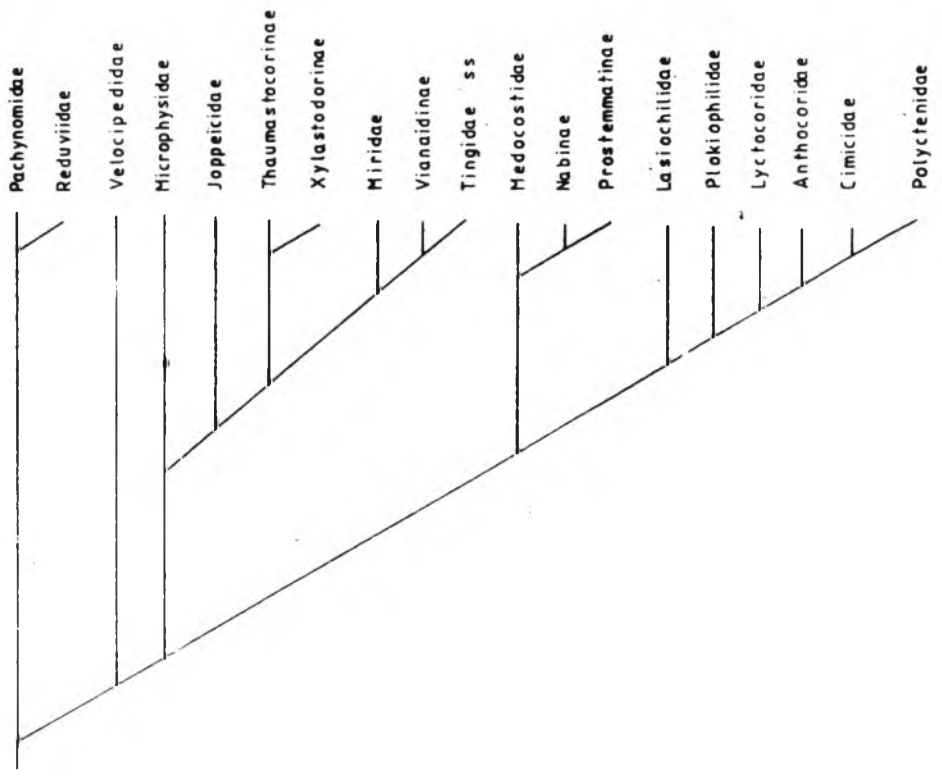


Fig. 28. The pattern of relationships of *Cimicomorpha* as proposed by SCHUH and ŠTYS (1991)

WOJCIECHOWSKI (1992) with a somewhat weaker discriminating value. It implies that, although the modification of the character occurs more than once in lower taxonomic units of a given clad and represents the result of the developmental parallelism or convergence, it is present only in a particular line, which can be precisely defined on the basis of the unquestionable apomorphies. Moreover, the character appears in the group only sporadically and is typical of a definite monophyletic group of close taxa. Accordingly, a secondary apomorphy cannot be used while defining taxonomic units of higher ranks (for example families) but plays a discriminating role in lower taxa (for instance while dealing with tribes or species groups). Such a secondary apomorphy can be illustrated, for instance, by the characteristic change in the

structure of antennal segment II in the genera *Alcecoris* McATEE and MALL. and *Sophianus* DIST. (which, however, is not distinctive of the subfamily *Isometopinae* and only sporadically occurs in other representatives of *Miridae*) or the tarsal segment number reduction. Although the latter has taken place in different developmental lines of *Heteroptera*, it can be also used in evaluating the relationships of *Isometopinae*, and it allows to separate, for instance, the genus *Gigantometopus* SCHW. and SCHUH into an independent developmental line.

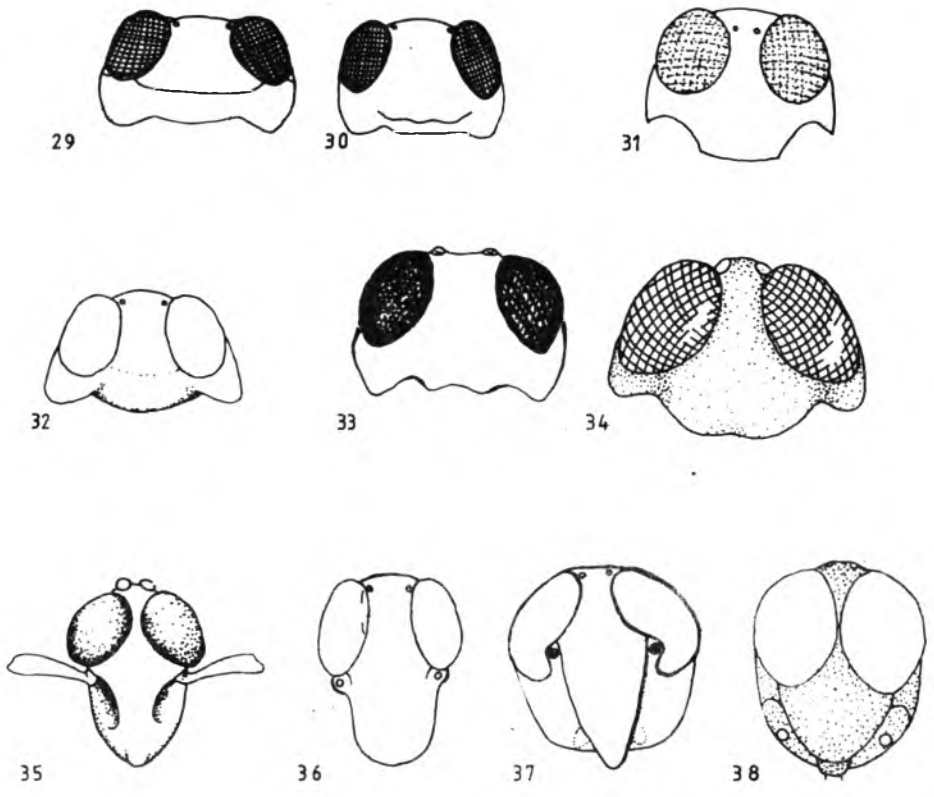
By introducting the notion of a secondary apomorphy we can enjoy more flexibility: cladistic analysis (HENNIG, 1950, 1966, 1981), with its strict use of synplesiomorphies and autapomorphies, formalized exceedingly the rules of constructing phylogenetic diagrams of different groups, including *Isometopinae*. Such a shortcoming must have been overcome by all authors who attempted to conduct the cladistic analysis (e.g. SCHUH, 1976). The analysis of apomorphies is further complicated by the fact that the characters are highly variable (especially within *Heteroptera*). Accordingly, also the evaluation of the relationships among the groups becomes more difficult regardless of the taxonomic level. Numerous contemporary authors have already paid attention to that restraint, but the method of overcoming it has not been worked out so far.

6.1. Head

The head structure in *Isometopinae* is peculiar when compared to other *Miridae*. The unique morphological character of this element has been noticed by numerous investigators. However, a detailed analysis of all the structural elements has not been presented so far.

While examining the head in *Isometopinae*, SCHUH (1976) described its structure as "modified, often flattened or elongated dorso-ventrally". However, it should be noted that variously advanced verticalization of head can be observed in many families of *Miridae (Cylapinae: Cylapini; Pylinae: Halticini; Mirinae: Pithanini)*. Thus, it seems that the character represents a developmental parallelism and it is difficult to comment on its value in phylogenetic studies within *Miridae*. Undoubtedly Schuh was right while claiming that not vertical head was plesiomorphic in relation to the dorso-ventral elongation condition. The structural type in which the head is higher than its width (Figs. 35—38) is described in the genera *Totta* GHAURI and GHAURI, *Alcecoris* McATEE and MALLOCH, *Wetmora* McATEE and MALLOCH, *Lidopiella* HENRY, *Myiopus* HENRY, *Sophianus* DIST. and some species of the genus *Myiomma* PUT. In other genera we observe a reverse situation, i.e. the

head is not so high as it is broad (Figs. 29—34). The condition is probably secondarily developed and it occurs in different developmental lines. Presently, it is difficult to evaluate how useful the character can be in phylogenetic analysis.

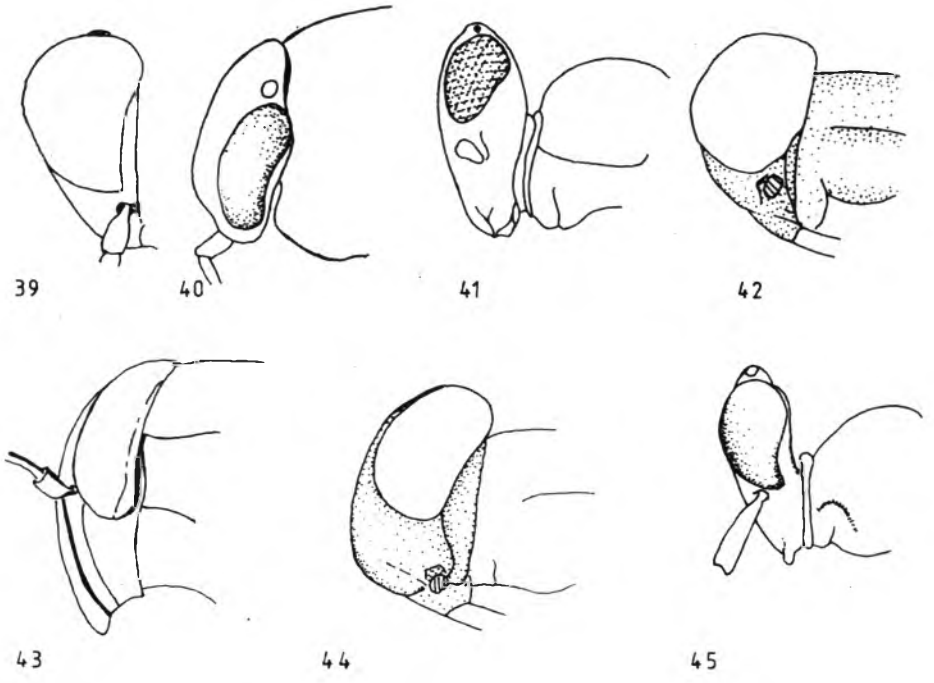


Figs. 29—38. The frontal part of the head capsule in some *Isometopinae*

29 — *Isometopus pictus*, 30 — *I. niger* (after LINNAVUORI, 1975), 31 — *Lindbergiolla auropilosa* (after CARVALHO, 1951), 32 — *Ptisca blattiformis* (after McATEE and MALLOCH, 1924), 33 — *Eurycrypha thanatochlamys* (after CARVALHO, 1976), 34 — *Magnocellus ghanaiensis* (after SLATER, 1976), 35 — *Sophiamus lamellatus* (after REN and YANG, 1988), 36 — *Wetmora nocturna* (after McATEE and MALLOCH, 1924), 37 — *Totta zaherii* (after GHAURI and GHAURI, 1983), 38 — *Myiomma ornatum* (after HENRY, 1979)

6.1.1. Position of head

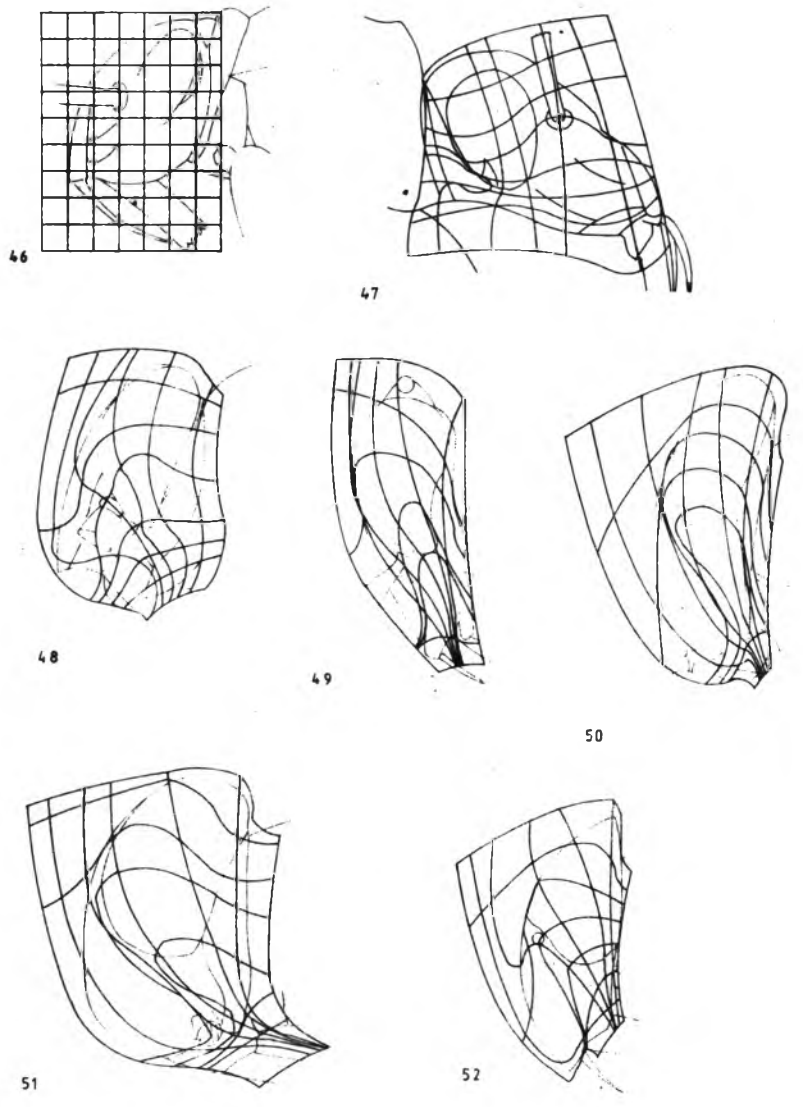
The change in head position from the prognathic or subprognathic into orthognathic with a tendency towards hypognathic must be regarded as apomorphic (Figs. 39—45). As a result of that modification the pharyngeal part is distinctively shorter and the eyes occupy a large part of the head. In most cases eyes are as long as the head itself. Such an advanced stage of



Figs. 39—45. Different variants of head and eye position in relation to pronotum
39 — *Myiomma fulva* (after SMITH, 1967), 40 — *Isometopus marginatus* (after REN and YANG, 1988), 41 — *Alcecoris globulosus* (after CARVALHO, 1951), 42 — *Myiomma capitatum* (after HENRY, 1979), 43 — *Totta zaheri* (after GHAURI and GHAURI, 1983), 44 — *Myiomma brasilianum* (after HENRY, 1979), 45 — *Sophianus lamellatus* (after REN and YANG, 1988)

the head orthognathic process in not found in other groups of *Miridiformes (Microphysidae* and *Thaumastocoridae)*. It has not taken place in the family *Nabidae* either; there the head clearly resembles the prognathic type. In *Miridae* a similar structural type of head is found in *Fulviini* UHLER and *Stenodemini* CHINA; in most other representatives (except *Isometopinae*) the head represents the type observed in *Calocoris* FIEB. (*Mirinae*). With the usage of allometric net (SOKAL, SNEATH, 1963), the latter head type was compared to that in *Isometopinae* (Figs. 46—52). The results indicated that the autapomorphic changes in the head structure in *Isometopinae* enhanced its orthognathic tendencies and the trend to bend backwards. It was assumed, thus, that an elongated head of the prognathic type represents a primitive, plesiomorphic condition.

When the head position in relation to pronotum is examined, it should be noted that in some genera of the subfamily *Isometopinae* head is strongly raised above the pronotal plane (*Alcecoris, Sophianus*). Such a condition results from an extremely strong dorso-ventral elongation of head (Figs. 41, 45). It must be regarded as apomorphic and discriminating



Figs. 46—52. The pattern of differences in head morphology in some *Miridae* representatives as obtained by allometric network results

46 — normal network against the outline of the head in *Calocoris (Mirinae)*, 47 — *Rhinomirus (Cylapinae: Fulviini); Isometopinae:* 48 — *Brailovskicoris nocturnus*, 49 — *Sophianus lamellatus*, 50 — *Isometopus* sp., 51 — *Myiomma brasilianum*, 52 — *Paratotta orientalis*

for the groups of genera. On the other hand, the condition observed in *Thaumastocoridae, Microphysidae* and *Nabidae* (as well as in most *Miridae*), in which head and pronotum lie more or less at the same plane, is plesiomorphic.

6.1.2. Frons and clypeus

It is unique for *Isometopinae* to have developed a complex of changes connected with the expansion of vertex and frons and their fusion. All this resulted in the formation of a uniform frontal plate. The expansion of frons is observed in all recent *Isometopinae* and proceeded in two main directions. The first tendency consists in the lateral expansion of frons (Figs. 29—34). It is observed in such genera as *Isometopus* FIEB., *Magnocellus* SMITH, *Eurycrypha* KIRK., *Linbergiolla* CARV., *Ptisca* McATEE and MALL., *Nesocrypha* KIRK., *Popovia* gen. nov. and *Paratopus* gen. nov. As a result of this process the frontal plate is formed. The plate encloses the eye and sometimes the eye slightly protrudes beyond the plate sides.

Within the second trend the frons expansion is directed ventrally and thus frontal plate does not enclose the eye, the sides of which extend well beyond the plate sides. Such a condition is observed in species of all other isometopinian genera, but in different groups different variants are developed. Frons is broad and not elongated in some species of the genus *Myiomma* PUT. and the genus *Myiopus* HENRY; it is narrow and strongly elongated, for instance, in the genera *Totta* GHA. and GHA. or *Paratotta* gen. nov. (Figs. 9, 35—38).

The process of frons expansion causes the shift of genae under the frontal plate and their tendency to be hidden under the expanding frons. It is especially well manifested within the first tendency. When the process proceeds along the second option (frons expands ventrally), the facial elements are also shifted but they remain exposed, i.e. visible in frontal view. Both, the process of frons modification and the shift of genae outside the frontal plate, are autapomorphic in *Isometopinae*.

In *Isometopinae* there is a tendency to shift clypeus onto the head underside. The process seems to have been initiated relatively recently because the Eocene forms had a normally developed clypeus (Fig. 7) and in most representatives of recent genera a shorter clypeus is still located at the lower margin of the frontal plate (Figs. 17, 21, 25, 35). The character cannot be regarded as apomorphic in the whole subfamily but only in a single developmental line. Clypeus is not reduced and clearly separated from the frons in all remaining representatives of *Miridae* and in the families which are closest related to *Miridae*. Accordingly, the condition can be regarded as plesiomorphic.

6.1.3. Eyes

The arrangement of facettes in the eye was analysed by COBBEN (1978) in 1st instar larvae of *Heteroptera*. The author concluded that the number

of ommatidia is variable in *Miridae* and no tendency can be indicated as useful in phylogenetic considerations. In the eye of adult *Miridae* the facettes lying close to one another and separated by narrow spaces seemed the most common type among *Miridae* and also in *Nabidae*. Among *Isometopinae* only in the genus *Diphleps* BERG. the eyes are differently structured: the facettes are well separated from one another and the lenses more protruding. The light reflexes make the eye look characteristically granular. It can be suspected that the former eye type (with the facettes almost contiguous) is plesiomorphic, while the latter modification represents an autapomorphic condition in *Diphleps* BERG.

Also the shape of eye seems informative for phylogenetic considerations. Precisely speaking, it is the shape of the inner eye margin that we are interested in. In most *Miridae* and in almost all *Isometopinae* inner eye margins are straight. This condition is regarded as plesiomorphic. In *Totta* and *Paratotta* there is a reniform incision on the inner eye margin (Figs. 9, 37). The condition is interpreted as a secondary apomorphy in *Isometopinae*, because it is also observed in some *Phylinae*.

In many *Miridae (Psallopinae; Phylinae: Hallodapinii* VAN DUZZE; *Isometopinae)* eyes are considerably enlarged. Such eyes are typical of most *Isometopinae*; however, in the genera *Joceliana* CARV. and *Aristotelesia* CARV. they are of the normal size. It can be suspected therefore, that the character changes independently in different developmental lines. This seems to be the reason why it has not been incorporated by most investigators into their phylogenetic considerations. Although some authors (SCHUH, 1976) regarded strongly enlarged eyes in males as an apomorphic condition in the subfamily, the size of eyes was not used while drawing phylogenetic conclusions in this study.

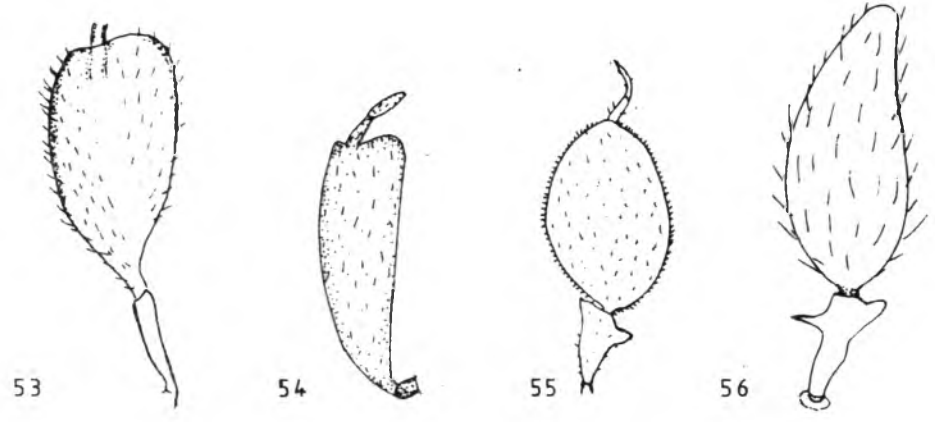
The position of eyes in relation to pronotum is not a stable character in *Isometopinae* either. In some species of the genera *Isometopus* FIEB., *Myiomma* PUT., *Nesocrypha* KIRK., *Wetmora* McATEE and MALL. and *Lidopiella* HENRY, the eyes reach proepipleurum (Figs. 20, 42), while in other genera they lie at a certain distance from it (Figs. 16, 26, 39, 40, 41, 43—45). Moreover, in some forms eyes reach upon pronotum dorsally (*Paratopus* HERCZ., *Lidopiella* HENRY), while in others they do not extend to its anterior margin (for instance, in *Jozefus* gen. nov. and in many species of the genus *Myiomma* PUT.). It seems possible that the position of eyes is relevant to determining phylogenetic relationships, but presently it is difficult to accept the character without further investigations.

Ocelli are present in all *Cimicomorpha* except female *Microphysidae* and *Miridae* (excluding *Isometopinae* and the genus *Diphleps* BERG.). The occurrence of ocelli is undoubtedly plesiomorphic. The absence of ocelli represents

an apomorphic condition, thanks to which (according to SCHWARTZ and SCHUH, 1984) *Psallopinae, Cylapinae, Phylinae, Mirinae* and *Bryocorinae* can be placed within a single clad.

6.1.4. Antennae

Most *Miridae* have a normally developed antennal segment I, which is not modified by the changes in length or shape. However, antennal segment I is modified (strongly shortened) in most representatives of *Isometopinae*, with the exception of the genera *Aristotelesia* CARV., *Plaumanocoris* CARV. and *Sophianus* DIST., where it is of normal length. The representatives of the genus *Alcecoris* McATEE and MALLOCH have developed peculiar structures on antennal segment I in form of characteristic spines. It seems that antennal segment I which is cylindrical, not shortened, and lacks additional surface structures, should be interpreted as plesiomorphic condition. Any changes in length, shape or structure are secondary and can occur independently in different developmental lines. The same holds true for the antennal segment II. The modifications of that segment must have taken place several times and occur in many variants (for example a club-like segment II in some species of the genus *Capsus* FAB., its spindle-like shape in *Heterotoma* LEP. and SEV. and *Atractotomus* FIEB. or spadulate in *Alcecoris* or *Sophianus*, Figs. 53—56). Accordingly, the modifications of that type can be at most regarded as secondary apomorphies which are characteristic of lower taxonomic units.

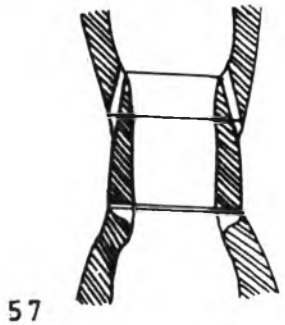


Figs. 53—56. Modifications of antennal segments I and II

53 — *Sophianus lamellatus* (after REN and YANG, 1988), 54 — *S. alces* (after DISTANT, 1910), 55 — *Alcecoris globulosus* (after CARVALHO, 1951), 56 — *A. periscopus* (after McATEE and MALLOCH, 1924)

The analysis of the antennal exoskeleton in *Heteroptera*, which was conducted by ZRZAWÝ (1990) revealed that there were some characters which

could be used in phylogenetic evaluations of suprageneric taxa. According to Zrzawý, the structure of two intersegmental sclerites is of vital significance; they are the preflagelloid, which is situated between pedicel and basiflagellum, and the intraflagelloid, which is located between basiflagellum and distiflagellum. Zrzawý distinguished several structural types of these elements with the plesiomorphic condition defined as preflagelloid and intraflagelloid in form of a thick-walled cylinder, which is approximately as broad as high, and its wall is thinner distally (Fig. 57). This type of preflagelloid and intraflagelloid (refe-



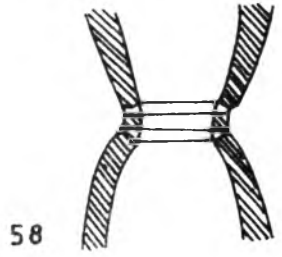


Fig. 57. The plesiomorphic condition of preflagelloid and intraflagelloid (after ZRZAWÝ, 1991)

Fig. 58. The apomorphic type of intraflagelloid (after ZRZAWÝ, 1991)

rred to as type I) occurs, for example, in *Thaumastocoridae* and *Microphysidae*. Among *Cimicomorpha* some apomorphic changes have appeared. One of them is reported in *Miridae* (it is classified by Zrzawý as type V) and consists in strong sclerotization and the shape changed into an annular structure (Fig. 58). In contrast to other *Miridae*, *Isometopinae* have the plesiomorphic type of preflagelloid (i.e. thick-walled and cylindrical). Alike other *Miridae*, on the other hand, they have an apomorphic intraflagelloid (i.e. sclerotized and annular). Thus, it must be suspected that modifications of preflagelloid and intraflagelloid took place independently from one another: initially, the structure of intraflagelloid was modified (apomorphic in *Miridae*) and subsequently that of preflagelloid was altered (apomorphic in the sister line of *Isometopinae*).

The position of antennae in *Isometopinae* is variable, although in most cases antennae are set below the lower eye margin. When compared with *Microphysidae*, *Thaumastocoridae* and *Nabidae*, the condition of antennal foveae located centrally and above the lower eye margin should be regarded as primitive (plesiomorphic). Among *Isometopinae* such a condition is reported only in the genera *Totta* GHA. and GHA. (Fig. 37), and *Paratotta* sp. nov. (Fig. 9). Posterior translocation of the antennal foveae in such a way that antennae

are set near the posterio-lateral head margin is also apomorphic in character (Figs. 39, 41, 44). Such a condition is typical of the genus *Myiomma* FIEB. and should be regarded as its autapomorphy.

6.1.5. Rostrum

Only one feature of the rostrum morphology has been included into phylogenetic considerations in case of *Miridae* — i.e. the length of the rostral segment I. According to SCHUH and ŠTYS (1991), elongated segment represents synapomorphy in the *Miridae—Tingidae* clad (in the authors' definition). All other *Cimicomorpha* have short rostral segment I (sometimes hidden by baccula), which was regarded as plesiomorphic. In *Miridae* the structure of rostral segment I is not further modified, so the character cannot be used while analysing the relationships within the family. However, in *Miridae* the first rostral segment can occupy different position in relation to the ventral side of the body. In most *Miridae*, including *Isometopinae*, rostral segment I at repose lies close to the lower head surface; however, in the latter group the head is strongly shortened and rostral segment I extends below the pharyngeal part and reaches some thoracic sternites. The only exception to the rule is observed in the genus *Diphleps* BERG., where rostral segment I not only lies close to the ventral head surface, but it runs in a special groove along its entire length there. Because the base of rostrum (rostral segment I) is accomodated in the groove on the head underside, only its narrow part can be seen in lateral view (Fig. 59). It can be assumed that the head without the groove to accomodate rostral segment I represents a plesiomorphic condition, while the development of groove is apomorphic.

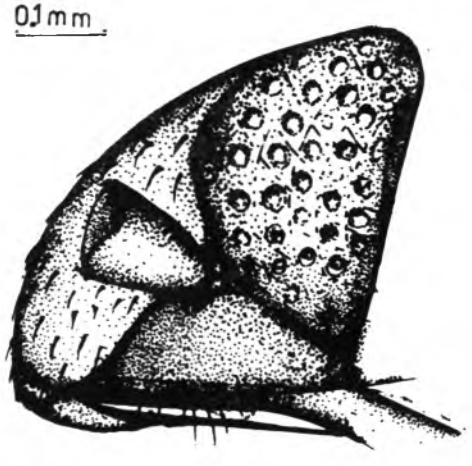


Fig. 59. Head in *Diphleps unica* in lateral view

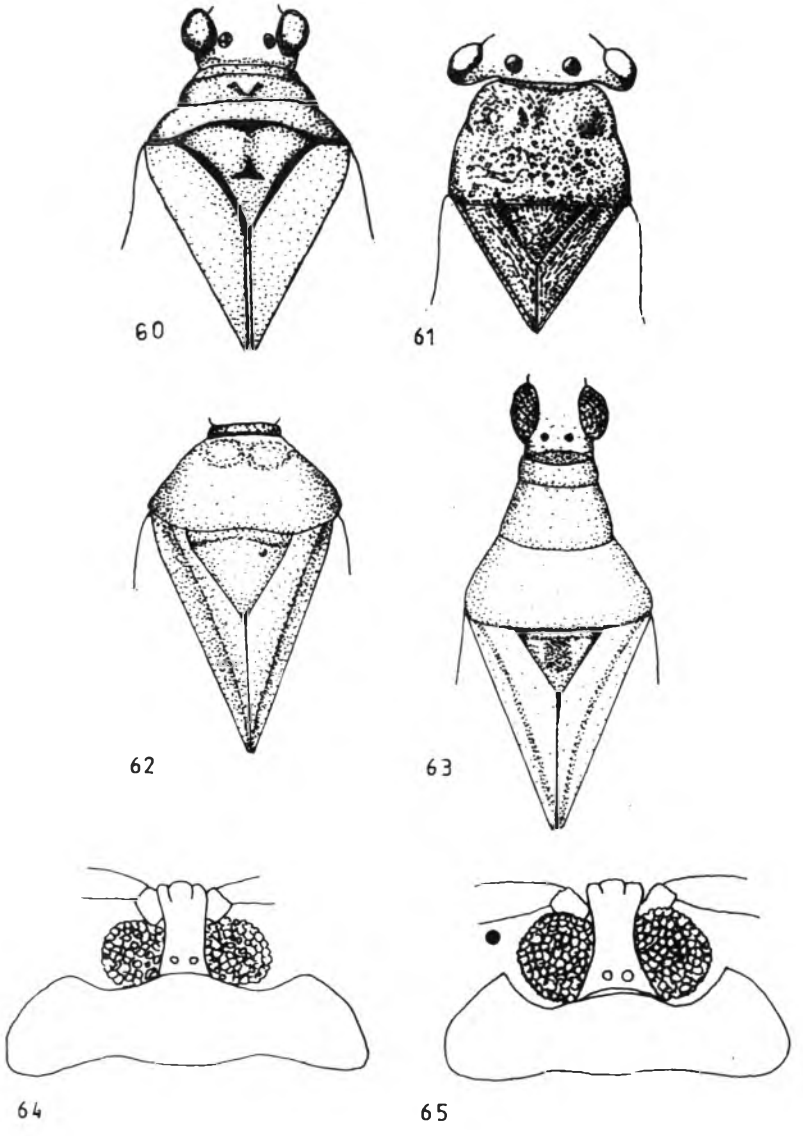
The length of rostrum is variable in *Isometopinae* even within single genera (for instance, different lengths are reported for *Isometopus* FIEB. and *Myiomma* PUT.). The fact that no apparent principles underlying those metric variations have been discovered so far makes the character useless while evaluating the relationships within the group.

6.2. Pronotum

In comparison to other mirid groups, pronotum in *Isometopinae* is, in many cases, significantly modified. Its anterior part is provided with a collar, the relevance of which to phylogenic decisions was discussed by SCHUH (1974, 1976) and SCHUH and SCHWARTZ (1984). The collar is developed in most *Miridae* (*Isometopinae*: *Blaumanocoris*, *Sophianus*, *Alcecoris*; *Cylapinae*: *Fulviini*, *Cylapiini*; *Mirinae*, *Bryocorinae*, some *Phylinae*: for instance *Acrorhinium* NAUL., *Azizus* DIST., *Laringulus* SCHUH, *Hallodapus* FIEB., *Systelonotus* FIEB.) as well as in *Thaumastocoridae*, *Microphysidae* and some *Nabidae* (Figs. 60—65). Accordingly, the occurrence of the collar may be either apomorphic (as suggested by SCHUH, 1974, 1976) or, which is equally probable, it can represent a plesiomorphic condition (developed even in some *Nabidae*). In the latter case the absence of collar due to reduction should be interpreted as apomorphy. Whatever the original condition was, its modification took place many times during the evolution of *Cimicomorpha*. Presently, it seems hardly possible to determine whether the character can be of the diagnostic value in any phylogenic considerations within *Cimicomorpha* (including *Miridae*).

Within *Miridae* the differences are reported also in the structure of the anterior part of pronotum. In most representatives of the family, and also in *Thaumastocoridae*, there are some symmetrical cushion-like protuberances called calli. Morphological differences among them (the occurrence or the absence of the median division, their location on the anterior part of pronotum, etc.) indicate that they not only might have developed independently in those groups, but that they even might not be homologous structures. In such an interpretation pronotum without calli in its anterior part is regarded as an original condition. However, the occurrence of various protuberances in different taxa indicates that they originated and developed independently (not necessarily as homologous structures). Accordingly, it is very difficult to define the character and use it in the analysis of the phylogenic relations.

The shape of the anterior margin of pronotum in *Miridae* constitutes an interesting trait to examine. In most mirids the anterior margin of pronotum is straight or slightly convex (as in related families); such a condition is interpreted as plesiomorphic. A differently shaped anterior margin of pronotum is described only in some *Isometopinae*, in which it is provided with a more or less sinusoidal incision (with the anterio--lateral corners advanced forward); such a condition is regarded as apomorphy.



Figs. 60—65. Modifications of the pronotum shape in some *Cimicomorpha*

60 — *Microphysidae* — *Loricula pselaphiformis* (after KELTON, 1980), 61 — *Thaumastocoridae* — *Onymocoris izzardi* (after DREAK and SLATER, 1956), 62 — *Miridae* — *Callocoris affinis* (after WAGNER, 1971, modified), 63 — *Nabidae* — *Nabis ferrus* (after KERZHNER, 1981, modified), 64 — *Diphleps unica* (after HENRY, 1977), 65 — *Diphleps maldonadoi* (after HENRY, 1977)

The anterior margin of pronotum is differently structured in the genus *Diphleps* BERG. The margin is bisinusoidally incised and the anterio-lateral corners of pronotum are shifted forward and enclose a considerable part of the head (Figs. 64, 65). Such a condition is not found in any other

group of *Miridae*. Nowhere has the shortening of the whole pronotum been so advanced as in the genus *Diphleps* BERG. either. In some species of the genus pronotum is four times as short as its width, with strongly flattened lateral fragments. Such a modification of pronotum can be undoubtedly interpreted as apomorphic in the species of the genus *Diphleps* BERG.

Differences in pronotum morphology are often observed at a specific level. For instance, some species of the genus *Myiomma* PUT. do not have laterally flattened parts although their congeners are all provided with them. Alike, a straight posterior margin of pronotum, or the one with a single or with two incisions, can also be found in different species of *Magnocellus* SMITH, *Corticoris* McATEE and MALL. and *Myiomma* PUT. These modifications in the structure of pronotum must have taken place many times. Presently, it is impossible to conclude on their relevance to the phylogenic considerations within lower taxonomic units.

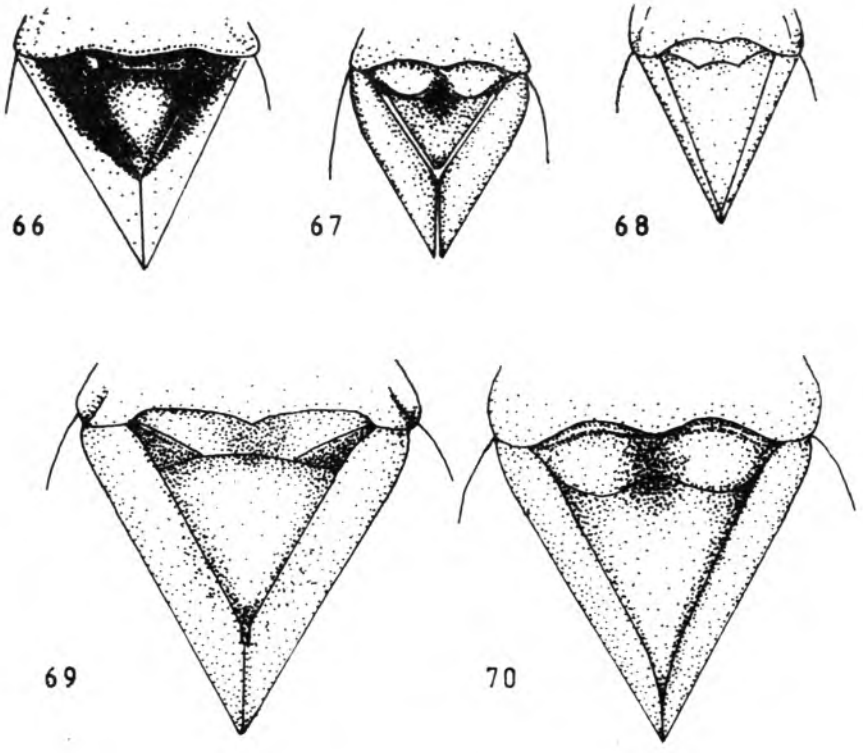
6.3. Mesonotum

In *Miridae* morphological differences involve the middle part of mesonotum, i.e. mesoscutum. In many *Miridae* mesoscutum is completely or almost completely hidden under pronotum (the condition, however, occurs only in the genera *Aristotelesia* CARV. and *Plaumanocoris* CARV. of the subfamily *Isometopinae*). A similar structural type has been developed in *Thaumastocoridae* and in most *Nabidae*, although in the latter (as in some genera of the subfamilies *Phylinae, Cylapinae, Mirinae*) and in most *Isometopinae* mesoscutum is exposed, i.e. it is not hidden under pronotum. The structural type of mesonotum is not a stable character either in different families of *Cimicomorpha* or within particular subfamilies of the family, so it cannot be used in phylogenic analysis. Neither is it possible to decide which condition is original.

Apart from these, the differences in structure of mesoscutum in *Isometopinae* include the occurrence of medial depression. However, as the character appears in different developmental lines, it can be of diagnostic value only for lower taxonomic units.

Scutellum in most *Miridae* (as in all other *Cimicomorpha*) takes form of a small, almost equilateral, slightly protruding triangle, which is separated by a transverse groove from mesoscutum (Figs. 12, 60—63, 66, 67). Such a condition is regarded as plesiomorphic. In *Isometopinae* scutellum

is either plesiomorphic or apomorphic. The modified scutellum is distinctly elongated (4—6 times as long as mesonotum whereas in the plesiomorphic condition scutellum is at most 3 times as long as mesonotum). An apomorphic scutellum is developed in *Nesocrypha, Popovia, Fronsonia, Jozefus, Paratopus, Isometopus, Magnocellus, Ptisca, Lindbergiolla* and *Eurycrypha* (Figs. 18, 24, 68—70).



Figs. 66—70. The variants of scutellum size, clavus shape and length of claval commissure: 66 — *Corticoris pintoi* (after HENRY, 1984), 67 — *Myiomma fulva* (after SMITH, 1967, modified), 68 — *Ptisca blattiformis* (after McATEE and MALLOCH, 1924), 69 — *Popovia fijiensis*, 70 — *Magnocellus ghanaiensis* (after SLATER and SCHUH, 1969, modified)

As indicated above, also a slight protuberance of scutellum is interpreted as a plesiomorphic condition. Within *Isometopinae* secondary modifications of scutellum are known only in the genera *Wetmora, Lidopus, Myiopus, Lidopiella, Brailovskicoris* and *Gigantometopus*, where it is strongly convex. Protruding scutellum is also reported in other subfamilies of *Miridae* in certain genera and in other families of *Cimicomorpha*. Accordingly, the character bears hardly any discrimination value while analysing phylogenetically higher taxonomic units.

6.4. Forewings

In general outline and in structure hemielytra in *Isometopinae* are similar to those in other *Miridae*. However, some morphological characters can be regarded as autapomorphic and employed while evaluating the relationships. For instance, the outer margin of hemielytra is sinuate incised at about one third of their length in *Brailovskicoris, Wermora, Lidopus, Lidopiella* and *Myiopus*. Some authors (CARVALHO, 1952; SCHUH, 1974) attributed this modification to mimetic processes (i.e. the processes by which an insect tries to become indistinguishable from its habitat in shape and colour). SCHUH (1974) stated that the changes connected with mimetic processes occurred independently and were not sporadical; he was convinced that they indicate a significant adaptive potential of *Miridae*. Simultaneously, however, Schuh was of the opinion that in many heteropteran groups convergent changes of the same type, which result from mimetic processes and influence the general appearance of insects, cannot be used as the only discriminating factors while defining higher taxonomic units.

In this case, our knowledge of the bionomy of *Isometopinae* is insufficient to determine whether the modification of the outer margin of hemielytra represents the convergence connected with mimetic processes or it is a developmental parallelism. It is, nevertheless, beyond any doubts that the sinusoidal incision of the forewing anterior margin represents a secondary modification, which is restricted to a single group of related genera within *Isometopinae* (and within *Miridae* it occurs only in *Pilophorini* DOUG. and SCOTT.). It can be regarded as a secondary apomorphy in these groups. The straight (or slightly convex) anterior margin of hemielytra can be regarded as plesiomorphic on the basis of its shape in other *Miridae* and in related families.

In *Thaumastocoridae, Microphysidae, Nabidae* and in most *Miridae* the clavus has parallel or slightly divergent sides (Figs. 12, 18, 66—68). Accordingly, at repose the line of wing contact forms a shorter or longer claval commissure (*commissura clavale*). A similar structure of wings is observed in many *Isometopinae*, among which there is only a sporadic tendency to reduce the claval commissure. Such a tendency is apomorphic. The reduction of claval commissure is differently advanced. The line is distinctly shorter in *Nesocrypha, Popovia, Fronsonia, Jozefus* and *Paratopus* (Figs. 18, 14), although the clavus sides remain parallel. On the other hand, in many species of the genera *Isometopus*, in *Magnocellus, Lindbergiolla, Eurycrypha* and *Ptisca* the line of wing contact is almost completely reduced and the clavus sides are convergent towards the apex (Figs. 24, 69, 70). It can be assumed that a total reduction of the claval commissure and the development of the clavus with convergent

sides is apomorphic in comparison to a partial reduction of the claval commissure length.

The occurrence or the lack of cuneus, which occupies the wing fragment behind the cuneal suture, was previously used in the analysis of the relationships within *Cimicomorpha*. According to KERZHNER (1981), SCHUH and ŠTYS (1991) the occurrence of cuneus is plesiomorphic and its absence represents an apomorphic condition. The cuneus is present in *Microphysidae* and in some *Nabidae (Velocipedinae)* as well as in all *Miridae*. It is absent from the wings in *Thaumastocoridae* and *Tingidae* (which are primitive groups in Kerzhner's definition) and also in *Reduvioidea* (which, in Schuh and Štys's opinion, constituted the earliest line to separate from *Cimicomorpha*). Accordingly, it does not seem possible to regard the occurrence of cuneus as plesiomorphic; instead, as the structure represents an addition to the original outline of the heteropteran wing, it is apomorphic in status. Thus, the character cannot be useful in the analysis of the relations among different families of *Cimicomorpha*, but it may prove informative within lower taxonomic units.

As indicated above, cuneus is always present in *Miridae* (except the strongly brachypterous forms) and its occurrence in an unmodified form should be interpreted as plesiomorphic in the family. Such a condition can be seen in *Gigantometopus*, in the known fossil genera (in which plesiomorphies are most numerous), in most recent genera of *Isometopinae* and in the remaining *Miridae*. As an exception to the rule within *Miridae*, in *Isometopinae* cuneus is strongly reduced in the genera *Plaumanocoris*, *Aristrotelesia* and *Joceliana*, and in the genera of *Nesocrypha* cuneus is enlarged (it extends beyond half membrane length). In neither case any modifications of the inner margin took place. Both, the reduction and the enlargement of the cuneus, should be regarded as apomorphic. Also the modification in the genus *Diphleps* is autapomorphic. The cuneus there is distally strongly incised in a sickle-like manner and enlarged. Due to that development the cuneus reaches almost the wing apex (Fig. 71).

Miridae have also developed some modifications of the hemielytra pubescence. Generally the hairs there are straight and setiform, which is commonly accepted as a plesiomorphic condition. Such pubescence is also typical of most *Isometopinae* and only in the genera *Wetmora*, *Brailovskicoris*, *Lidopus*, *Myiopus* and *Lidopiella* the hairs are transformed into spines, which are sparsely scattered on the hemielytra. Such hair modification is rather sporadic, but it sometimes occurs in other mirid groups as well. Accordingly, the character is interpreted as a secondary apomorphy in this group of species.

The microsculpture on hemielytra in *Miridae* takes form of wrinkles or densely distributed pits. SCHUH (1974) considered such a condition as plesiomorphic in the group. Most representatives of *Isometopinae* have a similar pattern of microsculpture and only in the genera *Wetmora*, *Lidopus*,

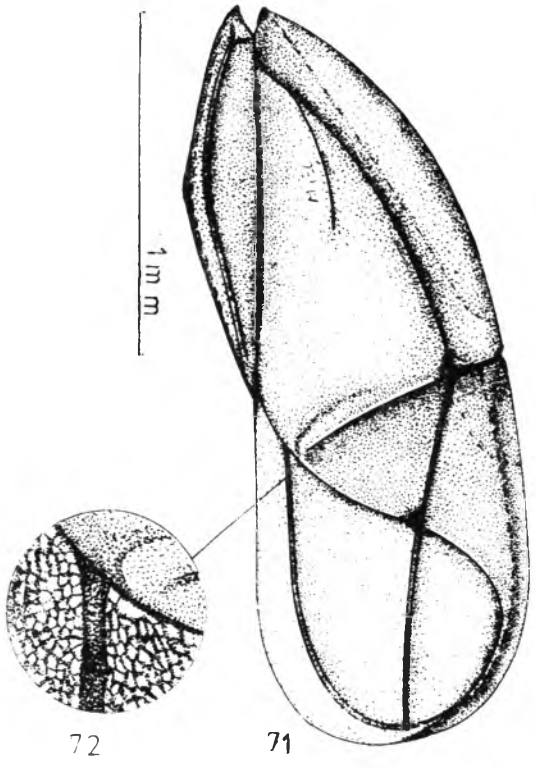


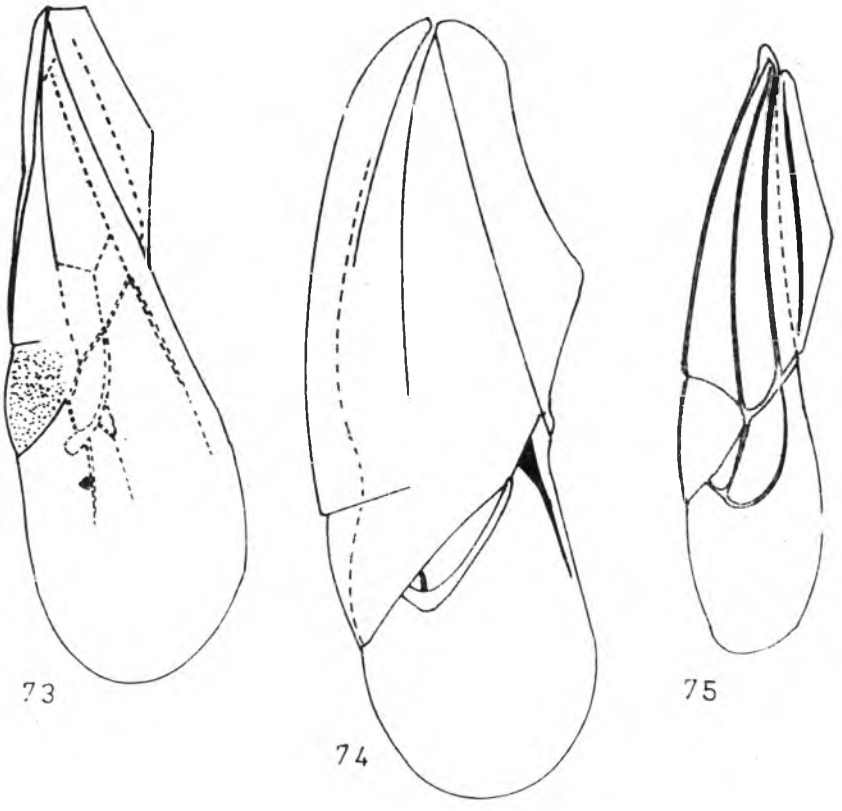
Fig. 71. Forewing in *Diphleps unica*
Fig. 72. A fragment of forewing membrane in *Diphleps unica*

Lidopiella, *Myiopus* and *Brailovskicoris* hemielytra lack microsculpture altogether. It can be assumed that the microsculpture in these forms was lost secondarily, so also the absence of microsculpture from the hemielytra in these genera should be interpreted as secondary.

In *Nabidae*, *Thaumastocoridae* and *Microphysidae* hemielytra are always opaque. This character is also most common among *Miridae*, with the only exception of some *Phylinae* and of the genus *Corticoris* within *Isometopinae*, where the hemielytra are semi-transparent. Therefore this condition should be regarded as a secondary apomorphy in the genus *Corticoris*.

The forewing membrane is generally smooth, delicate and longitudinally rugose. As such a membrane is typical of *Thaumastocorinae* and *Nabidae*, the condition should be regarded as original. A differently structured membrane is developed by *Diphleps* BERG. Its microsculpture is composed of more or less regularly shaped sixangular, conterminous cells (Fig. 72). It is a unique type of membrane microsculpture and it should be regarded as apomorphy in *Diphleps* BERG.

The venation of the sclerotized part of the forewing in *Miridae* is strongly reduced (like in many other families of *Cimicomorpha*). Generally, only subcosta (*Sc*) and a short radial-medial vein (*R*+*M*) are retained. The former sometimes delimits a wider or broader subcostal field *(area subcostalis?, embolium?)* and the latter coincides with MFL (median flexion line) at a certain distance and extends only to the half corium length (Figs. 73, 74). Among *Isometopinae* only in *Gigantometopus* vein *A*1 is retained in a vestigal form. In the genus *Diphleps* BERG. vein *A*1 is retained as well (Fig. 71). Undoubtedly the loss of veins is connected with the sclerotization of forewings and their transformation into hemielytra. This may explain why the reduction of venation took place so many times and independently in different



Figs. 73—75. Forewing

73 — *Microphysidae* — *Loricula elegantula* (after PERICART, 1972), 74 — *Isometopinae* — *Corticoris signatus* (after SCHUH and ŠTYS, 1991, slightly modified), 75 — *Mirinae* — *Calocoris affinis* (after WAGNER, 1971)

developmental lines. Accordingly, although it is clear that rich venation is plesiomorphic, the reduction of venation can be treated only as a secondary apomorphy with a very limited diagnostic value in phylogenetic deduction.

The pattern of veins on forewing membrane was an important feature in many phylogenetic studies on *Heteroptera* (for example, KERZHNER, 1981; SCHUH, ŠTYS, 1991). In *Miridae* (including *Isometopinae*) the forewing membrane is typically adorned with a single or with two closed cells (Figs. 74, 75). According to KERZHNER (1981) such a condition resulted from the reduction of the original four closed cells. In *Miridae* a small (anterior) closed cell is retained and three posterior ones have formed the larger one. Kerzhner believes that the process is further advanced in *Microphysidae*, in which only one of the middle cells is retained (Fig. 73). It also seems to indicate that in the latter family the processes of reduction took a different course when compared to that in *Miridae*. It should be noted that *Isometopinae* do not have a stable number of cells on forewing membrane. Some species of the genera *Isometo-*

pus, Lindbergiolla or *Myiomma* may have a single closed cell, while their congeners may have two closed cells on forewing membrane. It often happens that the smaller cell is so minute that it can be discerned only under the ideal light conditions. It can be assumed that in these genera the reduction of the smaller cell has not been completed yet. Presently, it seems impossible to incorporate this character into phylogenetic criteria.

In comparison to other representatives of *Miridae* (including *Isometopinae*) a different condition is found in the genus *Diphleps*, in which two gigantic cells almost cover the forewing membrane (Fig. 71). Such an extreme enlargement of these cells is regarded as an apomorphic condition in the group.

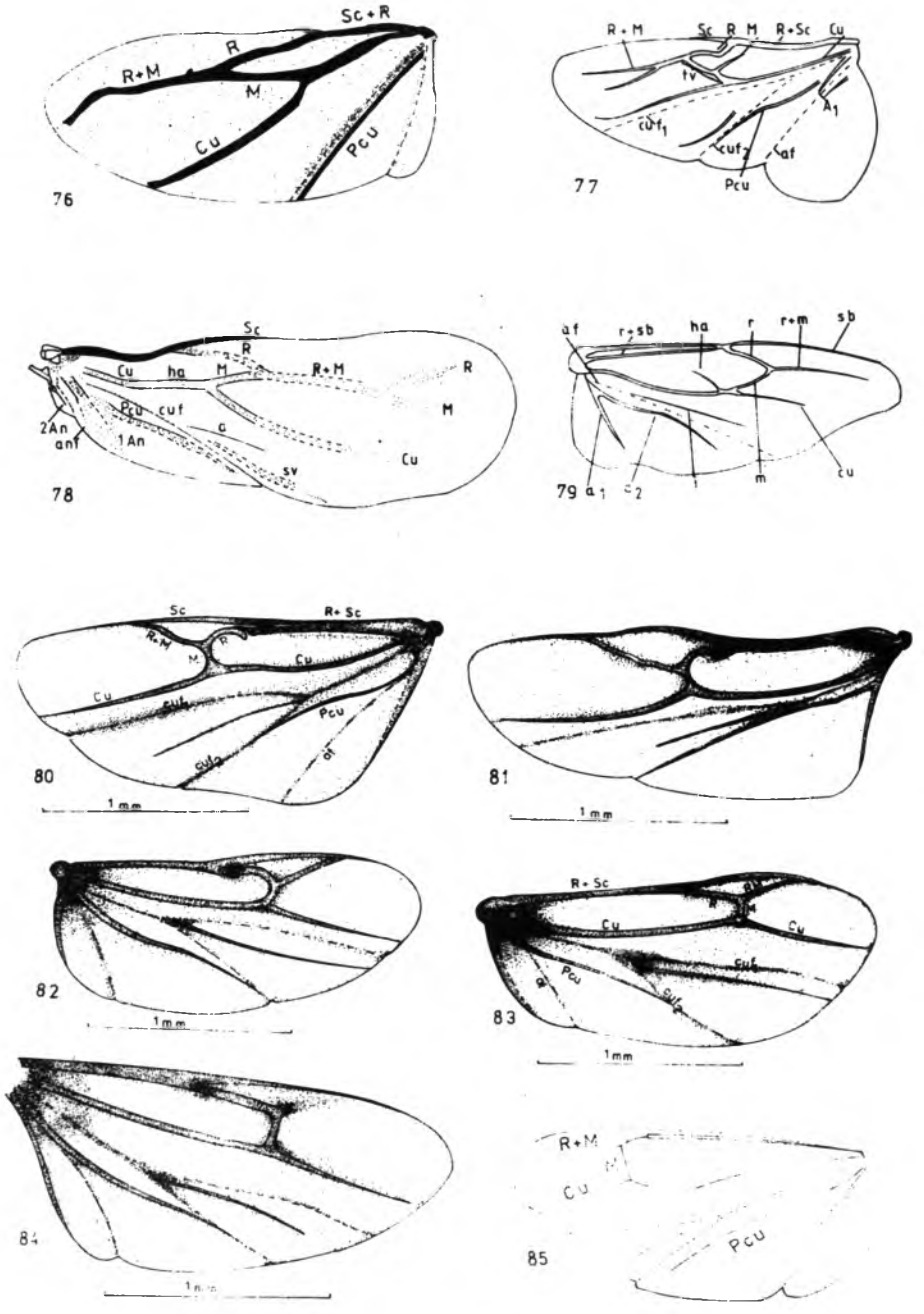
6.5. Hind wings

The hind wings in *Isometopinae* show some distinguishing characters in comparison to the ones in other *Miridae* and in other groups of *Miriformes*. These characters have not been used in any phylogenetic analysis of the subfamily so far.

In most families of *Cimicomorpha* vein $R+M$ runs as a single vein (as pointed out by SCHUH and ŠTYS, 1991) and it is forked apically (Figs. 77, 78) into separate veins R and M in *Nabidae* and *Microphysidae* (DAVIS, 1961; ŠTYS, 1962). Moreover, ŠTYS (1967) stated that $R+M$ forms several distal branches in *Mediocostidae*. In the family *Thaumastocoridae* the apical portion of $R+M$ remains undivided, alike in all *Miridae* (Figs. 76, 79).

Unlike that condition in other subfamilies of *Miridae*, vein $R+M$ in *Isometopinae* is relatively short and directed towards the outer wing margin (Figs. 80—83). In most cases the vein reaches the margin, but sometimes it is somewhat reduced (Fig. 84) and takes form of a stump-like process *(Nesocrypha, Popovia, Josefus, Fronsonia)*. In the remaining mirid groups (including the genus *Diphleps*) vein $R+M$ typically runs parallelly to the anterior wing margin (Figs. 79, 85). It should be noted that vein $R+M$, which is directed towards the wing margin or reduced, can be observed only in recent representatives of *Miridae*. Whenever it was possible to determine, in the *Isometopinae* materials in amber vein $R+M$ ran parallelly to the wing margin (as in *Electromyiomma* and *Archemyiomma*). Thus, the modification of vein $R+M$ course in recent *Isometopinae* cannot be interpreted as autapomorphic in the subfamily, but only as autapomorphic within the developmental line of the recent forms.

In the examined representatives of the genus *Psallops* (*P. grandoculus* LINN.), vein $R+M$ runs parallelly to the anterior wing margin (as in other *Miridae*).



Figs. 76—85. Hind wing structure in some representatives of *Cimicomorpha*

76 — *Thaumastocoridae* — *Baclozygum depressum* (after DREAK and SLATER, 1957, slightly changed), 77 — *Nabidae* — *Nabis ferrus* (after KERZHNER, 1981), 78 — *Microphysidae* — *Myrmydobia tenella* (after ŠTYS, 1962), 79 — *Miridae* — *Harpocera thoracica* (after WAGNER, 1971), *Isometopinae* (80—84): *Myiomma cixiiformis; Corticoris signatus; Lidopus heidemanni; Isometopus japonicus; Nesocrypha corticola;* 85 — *Diphleps unica* (after McATEE and MALLOCH, 1924, slightly modified)

Two other characters in hind wings seem to have a discriminating value in phylogenetic considerations. These are the shape of vein *R* and the shape of the closed cell formed by veins *R+Sc*, *R*, *M* and *Cu*. Both features seem to be independent. In *Taumastocoridae*, *Microphysidae* and (in a somewhat modified form, in *Nabidae* vein *R* is typically straight and relatively long (Figs. 76—78). A similar condition is observed also in the representatives of the tribe *Isometopini* (Figs. 83—84). In most *Miridae*, however, and in the tribe *Myiommini* of the subfamily *Isometipinae*, vein *R* is shortened and arcuate (Figs. 80—82). It can be assumed that the latter condition is secondary, and that a straight and long vein *R* is plesiomorphic.

Secondly, the closed cell on hind wing membrane is differently shaped in the representatives of the tribes *Isometopini* and *Myiommini:* its apical part is straight in the former and rounded in the latter (Figs. 80—84). The differences seem to be due to the length and position of vein *M* in relation to the anterior wing margin. It can be suspected that a normally developed vein which is vertical to the anterior wing margin represents the plesiomorphic condition.

6.6. Legs

In the subfamily femora are characteristically thickened. Such modifications have also been developed in *Psallopinae*, *Diphleps*, and some *Phylinae* (*Halticini* KIRK.). The thickening seems to be a saltatorial adaptation and must have occurred independently in different developmental lines. The fact that thickened femora were developed in different groups makes the apparent apomorphy weaker. Nevertheless, the condition is most stable in *Isometopinae*, and can be regarded as a secondary apomorphy within this subfamily.

Tibiae in *Isometopinae* do not exhibit any characters which might be used while evaluation phylogenetic relationships. Straight tibiae of the same diameter along the entire length seem to be plesiomorphic (as in *Thaumastocoridae* and *Microphysidae*). Differently shaped tibiae are relatively rare (as, for instance, the arcuate ones in *Plaumanocoris*) and such a condition can be used diagnostically at a generic level.

6.6.1. Femoral trichobotria

Femoral trichobotria, which were described by SCHUH (1975), represent an apomorphic condition in *Miridae* (SCHUH and ŠTYS, 1991). SCHUH (1975)

suggested that the occurrence of 6 trichobotria on femora II and 7—8 trichobotria on femora III was plesiomorphic in nature. According to him, an advanced reduction of these elements in *Isometopinae* (2 and 3 on femora II and III respectively) is autapomorphic in the group. Such an opinion agrees well with the principle of the polimeric occurrence of new organs followed by the processes of oligomerization (DOGIEL, 1929, 1936, 1954). When the numbers of femoral trichobotria were compared in different groups of *Miridae*, it turned out that the processes of oligomerization must have operated independently in different developmental lines. For instance, among the representatives of the tribe *Monalonini (Bryocorinae)* the number of femoral trichobotria ranges from 1 to 6 on femora II and from 1 to 7 on femora III. Trichobotria are fewer also in *Hyaliodini* CARV. and DRAKE (2+3 and 4+3), which belong to *Deraeocorinae* DOUG. and SCOTT and in some *Phylinae (Dicyphini* REUT., *Orthotylini* VAN DUZEE). The genus *Gigantometopus*, which was described in 1990, has femora II and III provided with 5 and 6 trichobotria respectively. It seems to represent the original condition. Accordingly, the reduced number of femoral trichobotria in *Isometopinae* can be interpreted as a secondary apomorphy.

6.6.2. Tarsus

The plesiomorphic condition is represented by a 3-segmented tarsus. Among *Isometopinae* a 2-segmented tarsus is a norm. The only exception is constituted by the genus *Gigantometopus*, in which tarsi are 3-segmented.

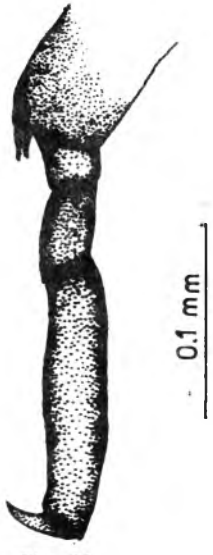


Fig. 86. Tarsus in *Diphleps unica*

A 2-segmented tarsus is also typical of *Thaumastocoridae*, and among *Miridae* it is observed in some *Cylapinae* (*Peritropis* UHLER, *Trynocoris, Hoewofulvius* SMITZ and ŠTYS, *Vanius* DIST., *Hemiophtalmocoris* POPP., *Bothriomiris* KIRK.) and in certain species of the subfamily *Bryocorinae* (*Hemisphaerodella* REUT.).

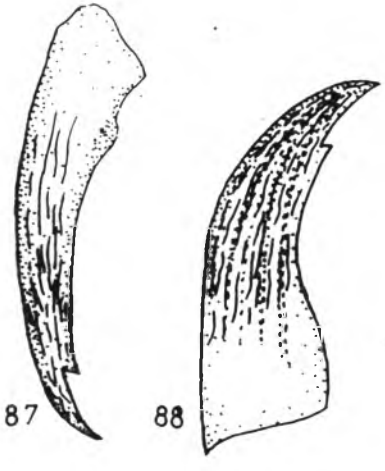
Diphleps representatives have 3-segmented tarsi (Fig. 86), in which the first segment is strongly shortened.

BERGROTH (1925) stressed the fact that the occurrence of a two-segmented tarsi in different groups cannot indicate close relation between them, because the character is sporadically observed also in various *Heteroptera*. SLATER and SCHUH (1974) suggested that 2-segmented tarsi are neotenic: they originated in the larval stage and persisted in adult forms. COBBEN

(1979) observed that a two-segmented tarsus was initial for *Heteroptera*, but this opinion has not been accepted by other authors. At present it is difficult to determine how two-segmented tarsi developed (they might as well have developed after the secondary reduction of the number of tarsal segments, when two first segments fused together). Nevertheless, the stability of the character in *Isometopinae* is so reliable, that the condition can be regarded as apomorphic and included into the phylogenetic analysis of the subfamily.

The structural elements on pretarsus in *Heteroptera* were analysed by several authors (DASHMAN, 1953; GOEL and SCHAEFER, 1970, 1979; SCHUH, 1976; COBBEN, 1968). COBBEN, GOEL and SCHAEFER called these structures "parempodia" and "pulvilli" instead of using the previous names "arolia" and "pseudoarolia" (KNIGHT, 1918). The most detailed analysis of these elements was presented by SCHUH (1976). The author expressed the opinion that setiform parempodia and the lack of pulvilli on the inner surface of the claw represented a plesiomorphic condition of the pretarsus in *Heteroptera*. The opinion is further confirmed by the fact that setiform parempodia bear a strong resemblance to mechanosensoric setae distributed on head, legs and other body parts in most *Hemiptera* (also pointed out by Schuh).

Setiform parempodia are observed in *Thaumastocorinae* (SCHUH, 1976), *Microphysidae*, *Nabidae* and among *Miridae*: in *Isometopinae*, *Psallopinae*, *Cylapinae*, *Deraeocorinae*, in some *Phylinae* and *Bryocorinae*. In other mirid groups modified types of these structures are developed. However, within a single subfamily (e.g. *Phylinae*) both types of parempodia can be observed, i.e. setiform and lamellar, and in other representatives of the family the structures are lost altogether (some *Cylapinae*). Accordingly, setiform parempodia are regarded as plesiomorphic and their reduction or modification as derived. The elements, however, are too diverse in structure to offer reliable information on the phylogeny of higher taxonomic units.



Figs. 87—88. Subapical tooth on claws
87 — *Myiomma fasciata;* 88 — *Popovia fijiensis*

Pulvilli are observed in different groups of *Heteroptera*, for instance in *Xylastodorinae* BARBER (*Thaunastocoridae*), *Oriini* CARAYON (*Anthocoridae*) and in certain *Miridae* (*Phylinae*, *Mirinae*, and some *Bryocorinae*). No pulvilli are reported in other groups of *Cimicomphora*. On this basis it can be assumed that the occurrence of pulvilli is a derived condition.

The presence of a subapical tooth on claws in some groups of *Miridae* (Figs. 87, 88) was reported by many authors (KNIGHT, 1918; McATEE and MALLOCH, 1924; CARVALHO, 1955; KELTON, 1959) and used as a discriminating character in certain taxa. SCHUH (1976) and SCHUH and SCHWARTZ (1984) were the first to include the character into phylogenetic studies within *Miridae*. According to those authors, the occurrence of the subapical tooth on claws in *Isometopinae, Psallopinae* and *Cylapinae* makes it possible to join them into a single clad, in which the character is synapomorphic. Although it can be accepted that *Psallopinae* are closely related to *Isometopinae* (as suggested by CARVALHO, 1956; SCHUH, 1974, 1976; HERCZEK and POPOV, 1993), it is hardly possible to agree that *Cylapinae* should be placed in the same clad. After analysing morphological details in the representative tribes of the subfamily (SCHMITZ and ŠTYS, 1973), it must be strongly suspected that *Cylapinae* are a heterogenic group. An extended analysis of the occurrence of the subapical tooth on claws revealed new data, in the light of which the validity of this character must be re-examined. The character is not so stable as it was previously believed. Neither *Gigantometopus rossi* nor the representatives of the genus *Diphleps* (the author's observation in *D. unica*) are provided with the subapical tooth on their claws. The element is absent from the claws in the genus *Cylapomorpha* POPP. (*Cylapinae: Cylapini*). On the other hand, the element is present in the subfamily *Psallopinae*. LINNAVUORI (1988) reported the occurrence of subapical tooth in *Pronotropis longicoris* (REUT.), *P. nasutus* REUT., *Macrotylus dentifer* WAG., *M. hymenocratti* PUCHK. and *M. brevirostris* (WAG.). All these data indicate that the element was developed independently in several developmental lines of *Miridae*. It can be assumed that the character holds its diagnostic value within lower taxonomic units and it can be regarded as a secondary apomorphy.

It should be noted that no structures corresponding to subapical teeth on claws were observed in *Thaumastocoridae, Microphysidae* or *Nabidae*. The absence of the element should be interpreted as a plesiomorphic condition in these groups.

The analysis presented above cannot be regarded as closed and final. With the new morphological data on *Heteroptera* and especially on *Miridae*, new characters can be revealed or their status re-evaluated.

7.

Relationships of *Isometopinae* FIEB.

To determine phylogenetic relationships and ranks of individual taxonomic units, the method of phylogenetic sequences was used. The method was proposed by NELSON (1972, 1973) and CROCRAFT (1974) and consists in obtaining phylogenetic sequences from cladistic schemes of relationships and transforming them into a classification. Within this system each taxon is a sister group in relation to the taxa of the same or lower ranks which are placed below. Thanks to the method the scheme of relationships presented in the cladogram can be accurately rendered without creating large numbers of higher categories (CROCRAFT, 1974).

Within *Cimicomorpha* the family *Miridae* constitutes a monophyletic group. The apomorphies shared by its representatives are distinctive enough to treat this unit as a family. The discriminating elements here include: asymmetrical, directed backwards parameres, trichobotria present on femora II and III, and also a single or two closed cells on forewing membrane (these cells developed in place of the original four cells: only the first one, which lies closest to the anterior wing margin, is retained, the remaining three merged forming the second closed cell). Additionally a divided trochanter seems to represent a discriminating character, as formerly suggested by KERZHNER (1981) and SCHUH and ŠTYS (1991). All these characters were incorporated by many authors in the studies on the phylogenetic relationships within *Cimicomorpha* (KERZHNER, 1981; SCHUH, 1975, 1976; SCHUH and ŠTYS, 1991).

It can be assumed that within *Miridae* two sister groups are constituted by two developmental lines (Fig. 96). The first line includes *Isometopinae*, while the second all other subfamilies which have been established so far (including *Diphlebinae*, which were previously placed within *Isometopinae*). *Isometopinae*

are recognized as a sister group because the constituent species shared distinctive autapomorphic characters. The forms belonging here have an orthognathic type of the head capsule (Figs. 39—45, 48—52) in which frons and a part of vertex lie almost vertically in relation to the body axis. In other *Miridae* that part of the head forms an angle with the body axis or it is almost parallel to it (as in some *Cylapinae* and *Mirinae*, Figs. 46, 47). The expansion and fusion of frons resulted in the clypeus being shifted onto the lower head surface and in extreme cases its position can be described as parallel to the long body axis and shifted towards the posterior head region (as in some species of the tribe *Isometopini*, Fig. 89). The processes of head expansion and development were discussed by SCHUH (1976).

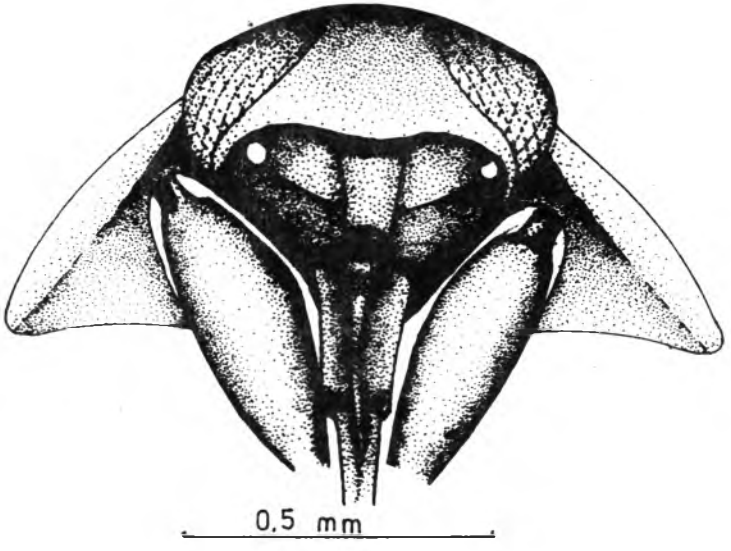


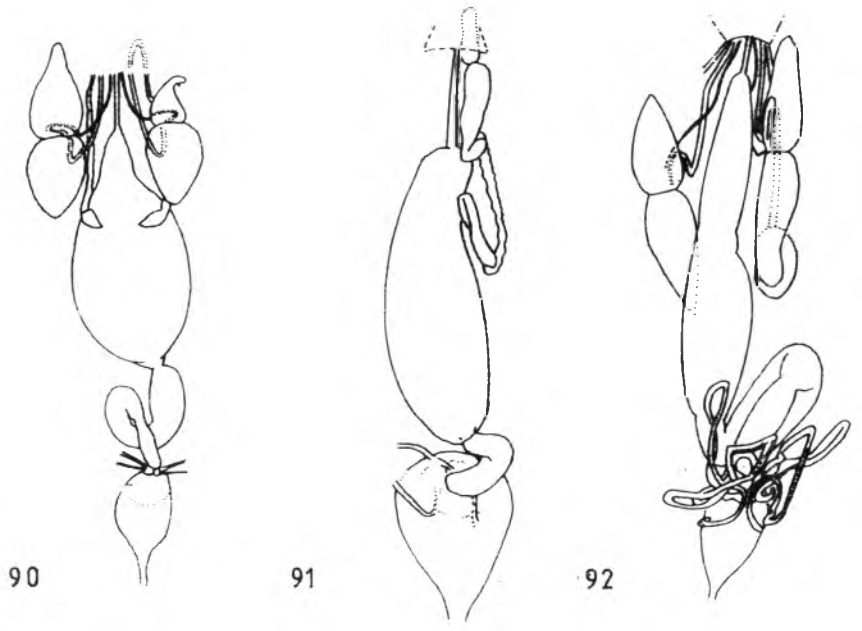
Fig. 89. Head underside in *Nesocrypha corticola*

All *Isometopinae* have retained ocelli. All *Miridae* lack ocelli, except for the genus *Diphleps* BERG., where they are present. The genus was described in 1924 and placed within the subfamily *Diphlebinae*, in family *Isometopidae* by Bergroth. The systematic decision was based on the occurrence of the ocelli, the short and broad pronotum, the long and sickle-shaped cuneus reaching the apex of forewing membrane and two veins on forewing membrane which, according to Bergroth, do not form closed cells. McATEE and MALLOCH (1924) defined the genus (together with the genus *Peritropis* UHLER) as intermediate between *Cylapinae* and the isometopidal forms, but they neither granted it a higher rank nor placed it within either unit. In the following study they relegated

Isometopinae to a rank of subfamily, but they held valid the tribal rank of *Diphleps*. Also other authors (for instance: ELYS, 1971; WHEELER and HENRY, 1977; HENRY, 1977, 1980; GHAURI and GHAURI, 1983) placed the genus within *Isometopinae*. However, it seems obvious that the occurrence of ocelli is plesiomorphic (they are present in most representatives of *Heteroptera*), whereas their reduction, which can be regarded as a secondary apomorphy, might have taken place several times (for instance in *Psallopinae*, which seem to be closely related to *Isometopinae*). In such cases the occurrence of a certain plesiomorphy alone cannot decide to which group the taxon is actually related. Both, the type of the head capsule (prognathic) and a well-marked clypeus, which enters the frons, connect the species of the genus *Diphleps* BERG. with all other *Miridae* and separate them from *Isometopinae*. The fact that ocelli are retained makes it possible to change the status of *Diphleps* BERG. into a subfamily *Diphlebinae* within the second developmental line (the sister group in relation to *Isometopinae*). In this aspect I share Bergroth's opinion and I believe that within the second developmental line they constitute a separate lineage. Such an assumption is confirmed by other morphological modifications observed in the representatives of the group and formerly described by many authors. Pronotum is strongly shortened, the inner margin of cuneus bears a sickle-shaped incision, cuneus almost reaches the apex of forewing membrane (Fig. 71). The autapomorphy in the genus include also a strong, lateral flattening of pronotum and the position of rostral segment I in a gutter-like groove on the head underside. As a result, only a small fraction is extended beyond the head capsule. Moreover, the genus *Diphleps* differs from other groups in a uniquely enlarged cells on forewing membranes and in the granular structure of the eye, resulting from increased distances among the facettes. The representatives of the genus have a 3-segmented tarsus (Fig. 86) and lack a subapical tooth on claws. The latter two confirm plesiomorphic nature of these characters. Morphological features (especially in the head structure) seem to indicate that in future the group might receive the status of a separate family.

Besides obvious discriminating traits, *Isometopinae* as a group share some secondary apomorphies. All the species belonging to the subfamily have thickened femora III and fewer femoral trichobotria on femora II and III. SCHUH (1975), basing on previous information, analysed the distribution and the number of trichobotria on legs in *Miridae*. He concluded that originally there were relatively many trichobotria (6 on femora II and 7—8 on femora III), but their number was reduced several times and independently in certain groups of *Miridae* (*Monalonini, Hyaliodiini*). The degree of reduction was most stable in *Isometopinae* (2 and 3 trichobotria on femora II and III respectively), which can be interpreted as a characteristic feature of the group.

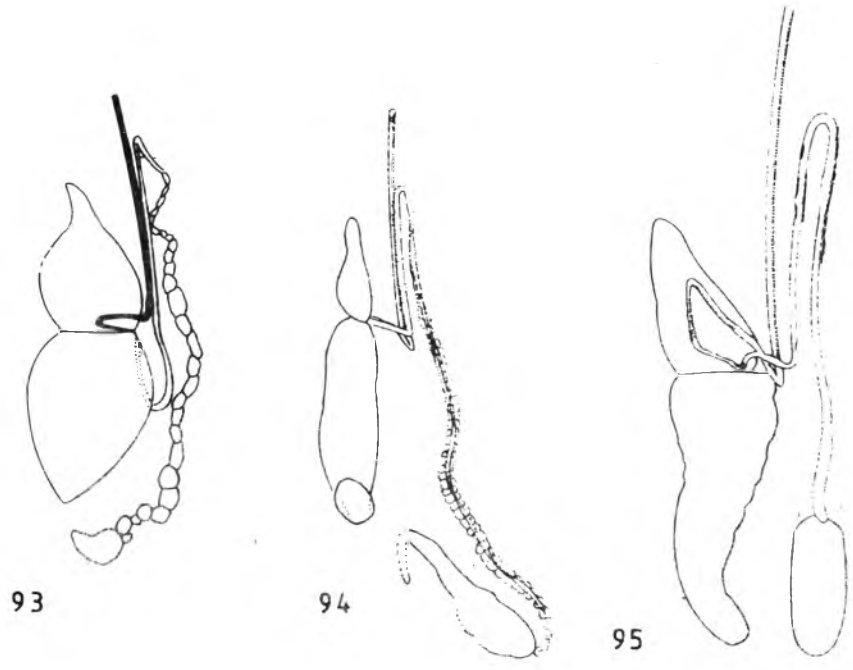
A separate status of *Isometopinae* is also confirmed by anatomical data provided by MIYAMOTO (1961). Although he concentrated on several genera only, he revealed that *Isometopinae* differ from other subfamilies of *Miridae* in certain details. For instance, the distal subdivision of their midgut is situated ventrally in relation to the stomach (Figs. 90—92), whereas it lies



Figs. 90—92. Morphology of the digestive system
90 — *Isometopus japonicus*, 91 — *Nabis apterus*, 92 — *Trigonotylus ruficornis* (after MIYAMOTO, 1961)

dorsally in all other mirid subfamilies. *Isometopinae* differ in morphology of the salivary gland ducts as well. The main salivary gland duct in the representatives of the subfamily forms a small coil, whereas it is almost straight in most other groups. The duct of the subsidiary salivary duct forms a loop behind its base and its distal half runs to the head capsule and is covered by enlarged transparent cells (Figs. 93—95) which absorb water (similar structures are reported in *Nabidae*, *Anthocoridae* and *Tingidae*). There are no such elements in any other mirid group. Accordingly, it can be assumed that the condition in *Isometopinae* is plesiomorphic.

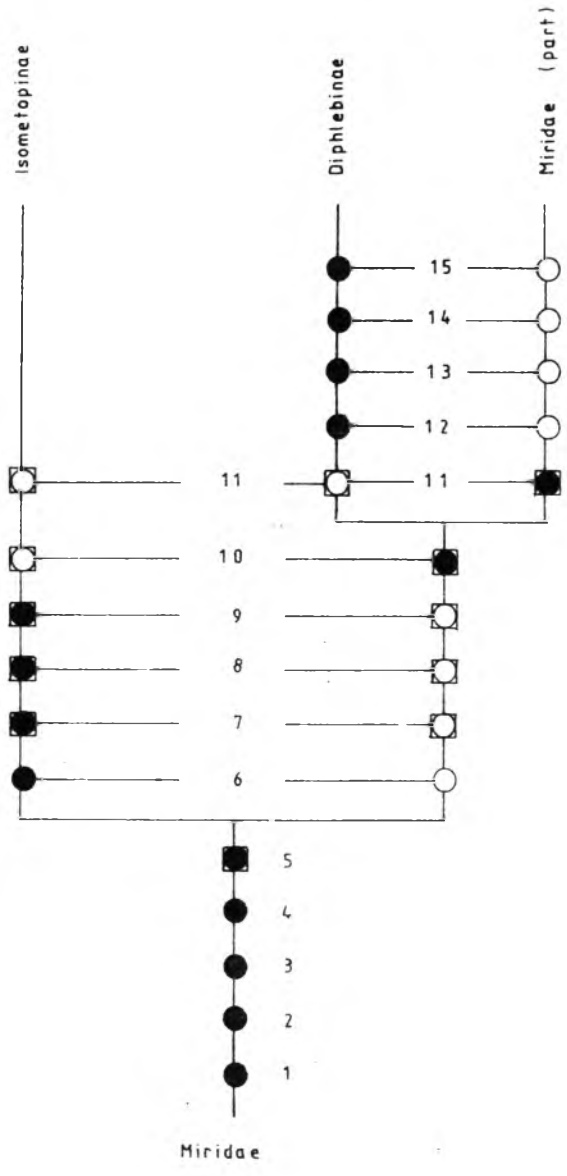
The analysis of the antenna exoskeleton is noteworthy as well. Such a study was conducted by ZRZAWÝ (1990). He stated that in *Isometopinae* the preflagelloid type (i.e. the type of the element which separates pedicel from basiflagellum) is much more primitive than the one in all other *Miridae* (Fig. 57), in which the type of preflagelloid represents an apomorphic condition (Fig. 58).



Figs. 93—95. The structure of the salivary gland
93 — *Isometopus japonicus (Isometopinae)*, 94 — *Nabis apterus (Nabidae)*, 95 — *Trigonotylus ruficornis (Mirinae)*

After analysing the morphology of recent *Isometopinae*, three distinct developmental lines can be defined (Fig. 97). The first line is constituted by the tribe *Gigantometopini*, in which a considerable number of plesiomorphies have been retained. The retention of 3-segmented tarsi should be mentioned as first. It is an exception to the rule within *Isometopinae*, and it can be observed only in *Gigantometopus* rossi SCHWARTZ and SCHUH. Both, the retention of vein *1A* on clavus and the absence of the subapical tooth from the claw, should be interpreted as plesiomorphic. Moreover, the genus representative has a reduced number of trichobotria on femora II (5) and III (6). Also the size of *Gigantometopus* individual (up to 7 mm) is remarkable because other members of the subfamily typically do not exceed 4 mm in length. The differences in size are so marked that the extreme enlargement of *Gigantometopus* can be interpreted as a secondary apomorphy (some forms as large *Gigantometopus* are also known in other mirid groups). To boot, the deep incision on pronotum, which is located between the calli, is also classified as a secondary autapomorphy.

The second developmental line contains two tribes. They have been distinguished on the basis of the type of clavus, the degree to which its sides are convergent and consequent occurrence or lack of the claval commissure.



Figs. 96. Cladogram of the relationships of recent *Isometopinae:* black circles — apomorphic conditions; black circles in squares — secondary apomorphic conditions; white circles — plesiomorphic conditions. The characters presented in Tab. 5

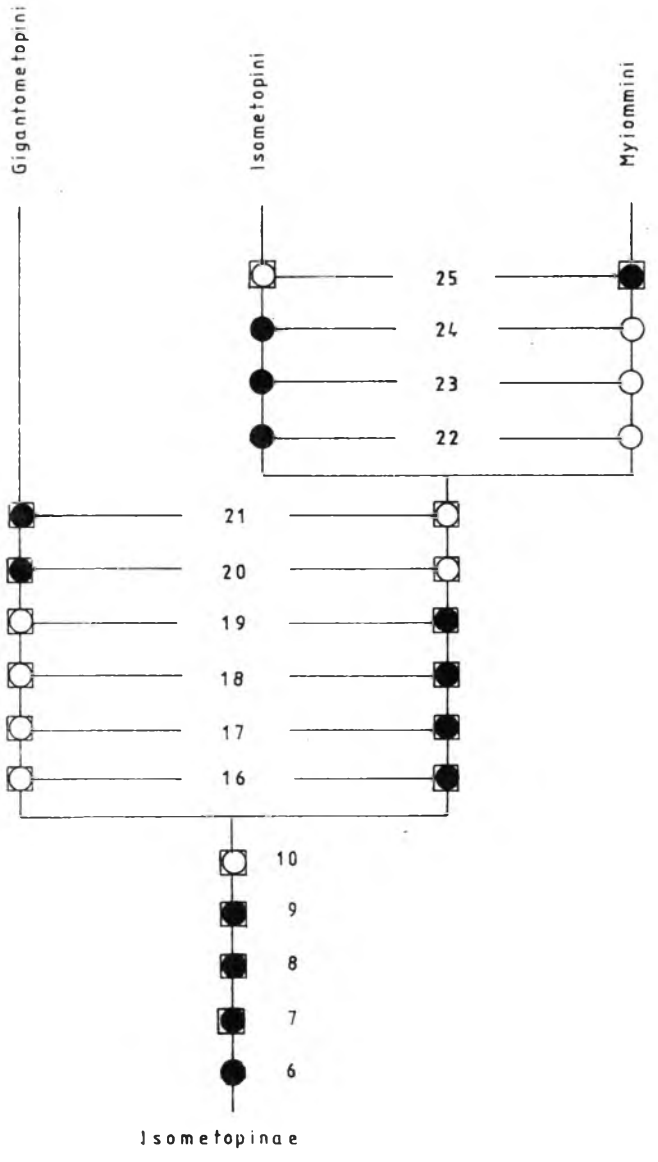


Fig. 97. Cladogram of the relationships of recent *Isometopinae;* the tribes of *Isometopinae:* black circles — apomorphic conditions; black circles in squares — secondary apomorphic conditions; white circles — plesiomorphic conditions. The characters presented in Tab. 5

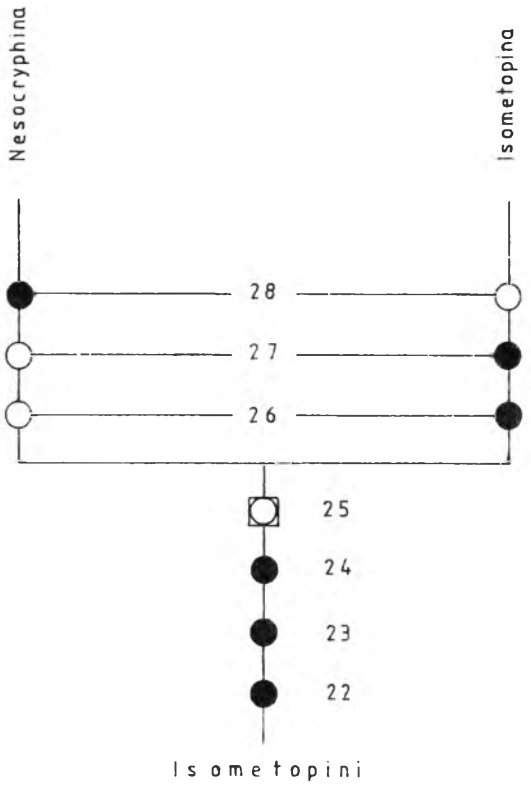


Fig. 98. Cladogram of the relationships of recent *Isometopinae;* partition of tribe *Isometopini:* black circles — apomorphic conditions; black circles in squares — secondary apomorphic conditions; white circles — plesiomorphic conditions. The characters presented in Tab. 5

Recent data on new genera (including information presented in this study), however, indicate that this character is not so stable as previously thought of and there are frequent cases of intermediate stages. Thus, the character cannot be accepted as discriminating at a tribal level. Decisive differences between the tribes can be observed in the morphology of head and in the structure of hind wings; on such basis the tribes *Isometopini* and *Myiommini* can be distinguished. The former contains the forms with the frons which is flattened frontally and strongly expanded laterally. The expanding frons shifts the genae and the clypeus under the frontal plate onto the lower part of the head capsule with the genae almost hidden and hardly visible in frontal view. In extreme cases (as in *Fronsonia, Nesocrypha*) the clypeus lies parallelly to the long axis of the body. The hind wings in *Isometopini* retain a plesiomorphic

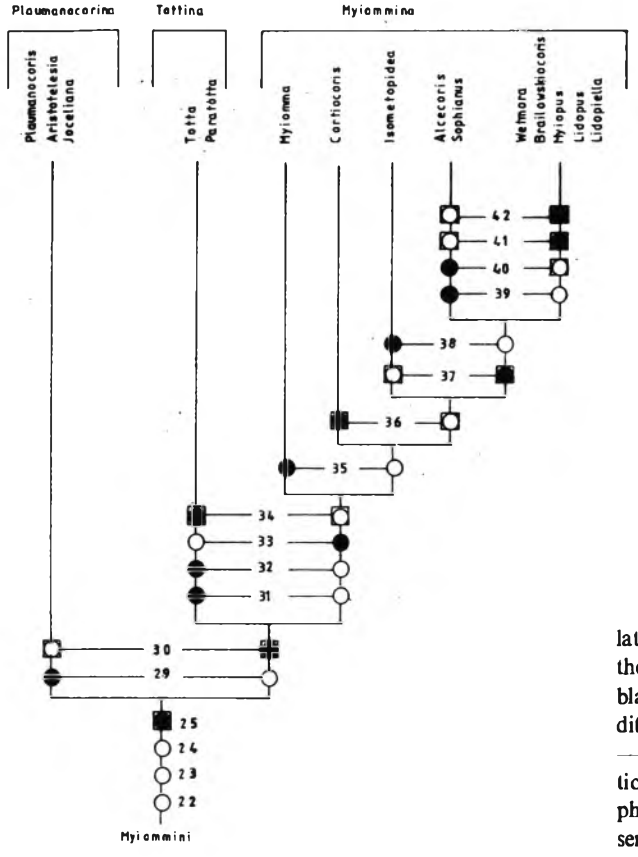


Fig. 99. Cladograms of the relationships of recent *Isometopinae;* the relationships within *Myiommini*: black circles — apomorphic conditions; black circles in squares — secondary apomorphic conditions; white circles — plesiomorphic conditons. The characters presented in Tab. 5

shape of the closed cell formed by the veins *R*+*Sc*, *R*, *M* and *Cu* (with vein *M* vertical in relation to the anterior wing margin) and the straight, not curved vein *R* (Figs. 83, 84).

The second tribe, *Myiommini,* contains the genera in which the plesiomorphic condition of the head structure has been retained. The genera of this tribe share the head structure with the frons not expanded laterally and the genae at least partly visible in frontal view. The modification of the head capsule in *Isometopini* is so peculiar that it could have hardly occurred more than once. The structure of hing wings in *Myiommini* is apomorphic. The species of the tribe have arcuate vein *R* and the apically rounded cell tip with strongly shortened vein *M* (Figs. 80—82). The characters indicate that both, *Isometopini* and *Myiommini*, are natural, monophyletic units.

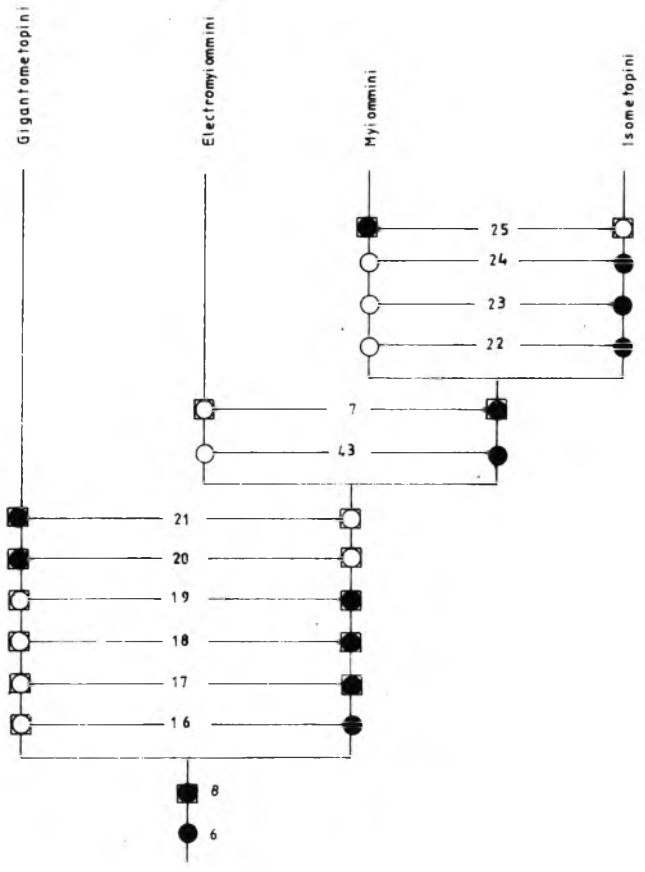


Fig. 100. The cladogram of relationships of *Isometopinae* including fossil taxa. Symbols as above

The tribe *Isometopini* splits into two developmental lines (Fig. 98). The first is constituted by the genera within the subtribe *Nesocryphina*. The species belonging to these genera *(Nesocrypa, Popovia, Fronsonia, Jozefus, Paratopus)* are provided with the clavus of almost parallel sides and with the claval commissure markedly shorter (more than 1.5 x) than the scutellum. The other autapomorphy in the subtribe is represented by the reduction of vein $R+M$ on hind wing into a stump-like process (Fig. 84).

The subtribe *Isometopina* holds a sister relation to *Nesocryphina*. The autapomorphies here include the loss of the claval commissure and a strong elongation of the scutellum, which reaches the inner corner of the forewing membrane base. Moreover, vein $R+M$ is not reduced on hind wing. The developmental line of *Isometopina* includes the following genera: *Isometopus, Magnocellus, Eurycrypha, Lindbergiolla* and *Ptisca*.

The tribe *Myiommini* is formed by three subtribes which seem to represent three independent developmental lines (Fig. 99). The first subtribe, *Plaumanocorina* (with the genera *Plaumanocoris, Aristotelesia* and *Joceliana*), shares an apomorphic condition of the reduced cuneus. In this group the pronotum characteristically overlaps the mesonotum, which can be regarded as a plesiomorphic condition. It should be noted here that our knowledge of the morphology of the constituent species is far from being complete. It can be suspected that with more data available, new generic groupings shall be formed.

Two subtribes, *Tottina* (with the genera *Totta* and *Paratotta*) and *Myiommina* (where the remaining genera were included) constitute the counterpart of *Myiommini*. This developmental line is characterized by a secondary apomorphy in form of an exposed mesoscutum and a plesiomorphic condition of the cuneus which is not reduced. In the subtribe *Tottina* frons is narrow and elongated and clypeus is completely fused with the frons. This type of frons is unique among *Isometopinae* — no other group shares these characters with *Tottina*. Also the reniform incision on the inner eye margin which lies at the same plane as antennal foveae might be interpreted as a secondary apomorphy. The fact that antennae arise above the lower eye margin, near the plane of the head symmetry, is regarded as plesiomorphic in the subtribe.

The subtribe *Myiommina* represents a sister group in relation to *Tottina*. The apomorphic condition here is realized by the position of antennae, which arise below the lower eye margin. In the genera of *Myiommina* clypeus is not fused with frons, frons is not narrowed and the inner eye margin is straight. The subtribe is further subdivided into five generic groups. The first group is constituted by a single genus *Myiomma*, which is distinguished by the fact that the antennae are set laterally, near the posterior head margin. An independent group is formed by the genus *Corticoris*, in which forewings are semi-transparent (a secondary autapomorphy). The remaining three groups share only a plesiomorphic condition of hemielytra, which are met in all the genera. This developmental line is divided into two sister groupings. The first one contains the genus *Isometopidea*, which is distinguished on the occurrence of a bowl-like depression on frons in front of ocelli. This character is interpreted as autapomorphy. The other developmental line receives the genera in which anterior margins of hemielytra are sinusoidally incised (a secondary apomorphic condition). A further partition results in formation of the group *Alcecoris* (containing the genera *Alcecoris* and *Sophianus*) and the group *Wetmora* (with the genera *Wetmora, Myiopus, Lidopus, Lidopiella* and *Brailovskicoris*). The former group is characterized by the autapomorphies in form of the head strongly raised above pronotum (Figs. 41, 45) and an advanced modification of antennal segment II (Figs. 53—56). The latter group has hairs on hemielytra strongly modified and the scutellum clearly raised, forming a pyramid in

extreme cases (e.g. *Wetmora*). A discriminating character of the group is constituted also by the fact that its members have no microsculpture on hemielytra, which is interpreted as apomorphy in *Isometopinae* (in all other genera of the subfamily dorsum is covered with microsculpture of diverse types).

In the light of presently available data, the relationships within *Isometopinae* can be presented in form of the cladograms in Figs. 96—100 and Table 5. I believe that it is necessary to continue the studies along these lines. All new facts and data must be incorporated into the system, so as to arrive at the natural classification, which would be based on the most accurately reconstructed phylogeny of the group.

Table 5

The list of plesiomorphic and apomorphic conditions used in constructing cladograms 96—100

	Plesiomorphic condition	Apomorphic condition
1.	More than 2 cells on forewing membrane	2 or 1 cell on forewing membrane
2.	Parameres symmetrical	Parameres asymmetrical, directed backwards
3.	No femoral trichobotria	Femoral trichobotria on legs II and III
4.	Trochanters undivided	Trochanters divided
5.	Intraflagelloid in form of a thick-walled cylinder with the diameter almost the same as its height	Intraflagelloid modified
6.	Head capsule of prognathic or subprognathic type	Head capsule of orthognathic type with a tendency to hypognathic modification
7.	Clypeus not reduced and not relegated from frons	Clypeus shortened and shifted from frons to underside of head
8.	Femora III not thickened	Femora III thickened
9.	Genae not shifted under the frontal plate	Genae shifted under the frontal plate
10.	Preflagelloid in form of a thick-walled cylinder almost as wide as high	Preflagelloid annular, short
11.	Ocelli present	Ocelli reduced
12.	Rostral segment I not depressed into the groove on the head underside	Rostral segment I in the groove on the head underside
13.	Inner margin of cuneus straight	Inner margin of cuneus sickle-shaped
14.	Pronotum not shortened, with sides not flattened	Pronotum strongly shortened, with sides strongly flattened
15.	Eye facettes touching one another	Eye facettes separated
16.	Tarsus 3-segmented	Tarsus 2-segmented
17.	Vein *1A* on clavus retained	Vein *1A* on clavus reduced
18.	Femoral trichobotria not reduced	Femoral trichobotria reduced

Table 5 cont.

	Plesiomorphic condition	Apomorphic condition
19.	No subapical tooth on claws	Subapical tooth on claws present
20.	Body size about 4 mm	Body size about 7 mm
21.	No incision between calli	Deep incision between calli occurs
22.	Frons convex, not expanded laterally	Frons flat, expanded laterally
23.	Claval commissure not shortened, less than 1.5 times as long as scutellum length	Claval commissure strongly shortened, at most 1.5 times as long as scutellum' length or missing
24.	Scutellum not enlarged	Scutellum strongly enlarged
25.	Vein *R* in hind wing elongated, straight; the cell formed by *Cu*, *M*, *R*, and *Sc*+*R* elongated, with rectangular apical part	Vein *R* in hind wing arcuately bent; the cell formed by *Cu*, *M*, *R*, and *Sc*+*R* with convex apical part
26.	Claval commissure partly retained	No claval commissure
27.	Scutellum not reaching the inner membrane corner	Scutellum reaching the inner membrane corner
28.	*R*+*M* on hind wing not reduced	*R*+*M* on hind wing reduced to a stump-like process
29.	Cuneus not reduced	Cuneus reduced
30.	Mesonotum hidden	Mesonotum exposed
31.	Clypeus not fused with frons	Clypeus fused with frons
32.	Frons not narrowed	Frons narrow, elongated
33.	Antennae set above the lower eye margin	Antennae set below the lower eye margin
34.	Eye with a straight inner margin	Eye with an incised inner margin
35.	Antennae set concentrically	Antennae set laterally, close to the poste-rio-lateral head margin
36.	Hemielytra not transparent	Hemielytra transparent
37.	Forewing with the straight or convex anterior margin	Forewing with the sinusoidally incised anterior margin
38.	No pit-like depression in front of ocelli	Pit-like depression present
39.	Head not raised above pronotum	Head strongly raised above pronotum
40.	Antennal segment II not modified	Antennal segment II strongly modified
41.	Hair on dorsum not modified	Hair on dorsum modified, spine-like
42.	Dorsum with punctae or wrinkles	Dorsum smooth
43.	Vein *R*+*M* on hind wing parallel to the anterior wing margin	Vein *R*+*M* on hind wing directed towards the anterior wing margin

8.

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Aleksander Herczek

Stanowisko systematyczne i stosunki pokrewieństwa w obrębie *Isometopinae (Miridae, Heteroptera)*

Streszczenie

Praca jest nowym spojrzeniem na związki filogenetyczne i stanowisko systematyczne podrodziny *Isometopinae (Miridae, Heteroptera)*. Przedstawiono w niej historię badań faunistycznych oraz poglądy na filogenezę grupy, poczynając od FIEBERA (1860), kończąc zaś na opracowaniach ostatnich lat. Następnie omówiono rozmieszczenie geograficzne form współczesnych, wskazując centra ich liczebności i różnicowania. W kolejnym rozdziale omówiono gatunki kopalne wraz z ich cechami charakterystycznymi. W dalszej części pracy opisano nowe taksony *Isometopinae*: gatunki, rodzaje, podplemiona i plemiona, podając cechy diagnostyczne. Następny rozdział poświęcono analizie cech morfologicznych *Isometopinae*, która stanowi próbę określenia ich plezjo- lub apomorficznego charakteru. Na podstawie przeprowadzonej analizy zaproponowano podział *Isometopinae*. Ustalono, iż w obrębie *Miridae* można wyróżnić dwie grupy siostrzane. Jedną stanowią *Isometopinae*, do drugiej należą pozostałe wyróżnione dotąd podrodziny (wraz z *Diphlebinae*, które były zaliczane do *Isometopinae*). *Isometopinae*, obejmujące współczesne gatunki, rozpadają się na trzy linie rozwojowe: *Gigantometopini*, *Isometopini* oraz *Myiommini*. Uwzględniając gatunki kopalne, można stwierdzić, iż tworzone przez nie plemię *Electromyiommini* stanowi grupę siostrzaną kladu *Isometopini-Myiommini*.

Aleksander Herczek

Systematischer Standpunkt und die Verwandschaftsverhältnisse auf dem Gebiet der *Isometopinae (Miridae, Heteroptera)*

Zusammenfassung

Diese Arbeit ist ein neuer Blick auf die phylogenetischen Verbindungen und auf den systematischen Standpunkt der Unterfamilie *Isometopinae (Miridae, Heteroptera)*. Im ersten Kapitel wurde die Geschichte der faunistischen Forschungen dargestellt und die Ansichten über die Philogenese der Gruppe, angefangen von FIEBER (1860) und mit den Bearbeitungen der letzten Jahre endend. Danach wurde die geographische Verteilung der gegenwärtigen Formen besprochen, unter Berücksichtigung ihrer Menge und ihrer Unterschiedlichkeit. Im folgenden Kapitel wurden die versteinerten Gattungen mit ihren charakteristischen Eigenschaften besprochen. Im weiteren Teil der Arbeit wurden die neuen taxonomen Einheiten der *Isometopinae* beschrieben: Gattungen, Sorten, Stämme, Unterstämme mit der Angabe ihrer diagnostischen Eigenschaften. Das nächste Kapitel wurde der Analyse der morphologischen Eigenschaften der *Isometopinae* gewidmet, die einen Versuch der Bezeichnung ihrers plesio- oder apomorphischen Charakters darstellt. Auf Grund der durchgeführten Analyse wurde eine Einteilung der *Isometopinae* vorgeschlagen. Es wurde festgestellt, daß man in dem Bereich der Miridae zwei schwesterliche Gruppen aussondern kann. Eine Gruppe bilden *Isometopinae*, zu der zweiten gehören die übrigen bis jetzt aufgezählten Unterfamilien (mit *Diphlebinae*, die zu *Isometopinae* gezählt wurden). Die Unterfamilie *Isometopinae*, die die gegenwärtigen Gattungen umfaßt, zerfällt in drei Entwicklungslinien: *Gigantometopini, Isometopini* und *Myiommini*. In Berücksichtigung der versteinerten Gattungen kann man feststellen, daß der sie umfassende Stamm der Electromyiommini eine schwesterliche Gruppe der Anordnung der *Isometopini-Myiommini* bildet.

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